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PROVISIONAL APPLICATION FOR PATENT COVER SHEET

This is a request for filing a PROVISIONAL APPLICATION FOR PATENT under 37 CFR 1.53(c).

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TITLE OF THE INVENTION (500 characters max)

COMPLETE BIOSYNTHETIC GENE SET FOR SYNTHESIS OF POLYKETIDE ANTIBIOTICS, INCLUDING THE ALBICIDIN FAMILY, RESISTANCE GENES, AND USES THEREOF

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Respectfully submitted,

SIGNATURE [signature]

Date 10/18/2002

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REGISTRATION NO. *(if appropriate)* 29,329

Docket Number: 79-1

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Number 2 of 2

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Attorney Docket 79-1

In the UNITED STATES PATENT and TRADEMARK OFFICE

APPLICATION OF M. ROYER, D. W. GABRIEL, R. FRUTOS AND P. ROTT

COMPLETE BIOSYNTHETIC GENE SET FOR SYNTHESIS OF POLYKETIDE ANTIBIOTICS, INCLUDING THE ALBICIDIN FAMILY, RESISTANCE GENES, AND USES THEREOF

TECHNICAL FIELD

The invention is in the field of genetic engineering, and in particular the isolation and expression of the biosynthetic genes that produce a family of antibiotics known generically as albicidins.

BACKGROUND OF THE INVENTION

U.S. Patent No. 4,525,354 to Birch and Patil described a "non-peptide" antibiotic of M.W. "about 842" called "albicidin". Albicidin is described as produced by culturing chlorosis-inducing strains of *Xanthomonas albilineans* isolated from diseased sugarcane, and mutants thereof. The antibiotic was isolated from the culture medium by adsorption on resin and was purified by gel filtration and High Performance Liquid Chromatography (HPLC). The chemical structure of this antibiotic was not determined and remained unknown, although the Birch and Patil patent disclosed spectral data for a fraction having antibiotic activity and the presence of approximately 38 carbon atoms and at least one COOH group. The present invention describes and characterizes the family of antibiotics that is produced by culturing chlorosis-inducing strains of *X. albilineans* and mutants thereof, together with the complete set of twenty biosynthetic genes capable of producing the unique and previously uncharacterized family of antibiotics produced by *X. albilineans* and previously lumped together as "albicidins". The set of twenty biosynthetic genes isolated, purified and cloned from a culture of *X. albilineans* revealed that this set of biosynthetic genes is capable of synthesizing products exhibiting a high level of variation among the products, indicating that albicidins comprise a family of polyketide antibiotics. The albicidins described in the present invention are synthesized by twenty genes, including one polyketide-peptide synthase, one polyketide synthase and two peptide synthases, but the substrates of the polyketide-peptide synthase and of one peptide synthase are not α-amino acids. The biosynthetic enzymes represent a previously undescribed and unique polyketide antibiotic biosynthetic system.

Xanthomonas albilineans is a systemic, xylem-invading pathogen that causes leaf scald disease of sugarcane (interspecific hybrids of *Saccharum* species) (Ricaud and Ryan, 1989 ; Rott and Davis, 2000). Leaf scald symptoms include chlorosis, necrosis, rapid wilting, and plant death. Chlorosis-inducing strains of the pathogen produce several toxic compounds. The major toxic component, named albicidin, inhibits chloroplast DNA replication, resulting in blocked chloroplast differentiation and chlorotic leaf streaks that are characteristic of the plant disease (Birch and Patil, 1983, 1985b, 1987a and 1987b). Several studies established that albicidin plays a key role in pathogenesis and especially in the development of disease symptoms (Wall and Birch, 1997; Zhang and Birch, 1997; Zhang *et al.*, 1999; Birch, 2001).

The prior art indicates that albicidin inhibits prokaryotic DNA replication and is bactericidal to a range of gram-positive and gram-negative bacteria (Birch and Patil, 1985a). Albicidin is therefore of interest as a potential clinical antibiotic (Birch and Patil, 1985a). However, low yield of toxin production in *X. albilineans* has slowed down studies into the chemical structure of albicidin and its therapeutic application (Zhang *et al.*, 1998). The chemical structure of this albicidin remains unknown, however this albicidin has been partially characterized as a non-peptide antibiotic with a molecular weight of about 842 that contains approximately 38 carbon atoms with three or four aromatic rings, at least one COOH group, two OCH3 groups, a trisubstituted double bond and a CN linkage (Birch and Patil, 1985a; Huang *et al.*, 2001).

Molecular cloning and characterization of the genes governing the biosynthesis of albicidin is of considerable interest because such information indicates approaches to engineer overproduction of albicidin, to characterize its chemical structure, to allow therapeutical applications and to clarify the relationship between toxin production and the ability to colonize sugarcane. Two similar mutagenesis and complementation studies have been conducted to identify the genetic basis of albicidin production in *X. albilineans* strains isolated in two different geographical locations, Australia and Florida.

One study of *X. albilineans* strain LS155 from Australia revealed that genes for albicidin biosynthesis and resistance span at least 69kb (Wall and Birch, 1997). Subsequently, three genes required for albicidin biosynthesis were identified, cloned and sequenced from two Australian strains of *X. albilineans* (LS155 and Xa13): *xabA*, *xabB* and *xabC* (Huang et al., 2001; Huang et al. 2000a, 2000b). The *xabB* gene encodes a large protein with a predicted size of 525.6 kDa, with a modular architecture indicative of a multi functional polyketide synthase (PKS) linked to a nonribosomal peptide synthetase (NRPS) (Huang *et al.*, 2001). The *xabC* gene, located immediately downstream from *xabB*, encodes an S-adenosyl-L-methionine (SAM)-dependent *O*-

methyltransferase (Huang *et al.*, 2000a). The *xabA* gene, located in another region of the genome, encodes a phosphopantetheinyl transferase required for post-translational activation of PKS and NRPS enzymes (Huang *et al.*, 2000b).

These first results demonstrated that the albicidin biosynthesis apparatus is a PKS and/or NRPS system. Such systems assemble simple acyl-coenzyme A or amino acid monomers to produce polyketides and/or nonribosomal peptides (Marahiel *et al.*, 1997; Cane, 1997; Cane and Walsh, 1999). These metabolites form very large classes of natural products that include numerous important pharmaceuticals, agrochemicals, and veterinary agents such as antibiotics, immunosuppressants, anti-cholesterolemics, as well as antitumor, antifungal and antiparasitic agents. Genetic studies of prokaryotic PKS and NRPS produced detailed information regarding the function and the organization of genes responsible for the biosynthesis of polyketides and nonribosomal peptides. Such knowledge, in turn, made it possible to produce combinations of PKS and NRPS genes from different microorganisms in order to produce novel antibiotics (McDaniel *et al.*, 1999; Rodriguez and McDaniel, 2001; Pfeifer *et al.*, 2001). Investigating the complete albicidin biosynthesis apparatus is therefore of great interest because such results may contribute to the knowledge as to how PKS and NRPS interact and how they might be manipulated to engineer novel molecules.

A second study with *X. albilineans* strain Xa23R1 from Florida revealed that at least two gene clusters, one spanning more than 48 kb, are involved in albicidin production (Rott *et al.*, 1996). This conclusion was based on the following data: (I) fifty Xa23R1 mutants defective in albicidin production were isolated; (ii) a Xa23R1 genomic library of 845 clones, designated pALB1 to pALB845, was constructed; (iii) two overlapping DNA inserts of approximately 47 kb and 41 kb, from clones pALB540 and pALB571 respectively, complemented forty-five mutants and were supposed to contain a major gene cluster involved in albicidin production; (iv) a DNA insert of approximately 36 kb, from clone pALB639, complemented four of the five remaining mutants not complemented by pALB540 and pALB571, and was supposed to contain a second region involved in albicidin production; and (v) the remaining mutant, AM37, which was not complemented by any of the three cosmids pALB540, pALB571 and pALB639, was supposed to be mutated in a third region of the genome involved in albicidin production.

The DNA sequences of all of the genes required to produce the albicidin family of polyketide antibiotics, the expressed protein amino acid sequences of all of the genes and the deduced structure of Albicidin have not been previously reported, although fragmentary sequences that include three of the biosynthetic genes have been reported. Identification of one albicidin gene, *xabC*, as a methyltransferase gene involved in albicidin biosynthesis is reported

by Huang, G., Zhang, L. & Birch, R.G. (2000a, Gene 255, 327-333) and claimed as biologically active in producing a polyketide antibiotic in PCT WO 02/24736 A1. Identification of a second albicidin gene, *xabA*, as a phosphopantetheinyl transferase gene is reported by Huang, G., Zhang, L. and Birch, R.G. (2000b) Gene 258, 193-199 and claimed as biologically active in producing a polyketide antibiotic in PCT WO 02/24736 A1. Huang, G., Zhang, L. & Birch, R.G. (2001) Microbiology 147, 631-642, report a DNA sequence of *xabB* (GenBank accession # AF239749), a multi functional polyketide-peptide synthetase that may be essential for albicidin biosynthesis in *Xanthomonas albilineans*. This *xabB* gene is reported as full length by Birch in PCT WO 02/24736 A1 (their seq. ID #1) and claimed by Birch in PCT WO 02/24736 A1 as a biologically active polyketide synthase of 4,801 amino acids in length, enabling production of albicidin. However, the DNA sequence reported by Huang et al (2001) in GenBank AF239749 and by Birch in PCT WO 02/24736 A1 (their seq. ID #1) appears to be incomplete and missing 6,234 bp of DNA sequence encoding 2,078 amino acids. We claim the complete DNA sequence of *xabB* (*albI*, our seq. 20) as 20,637 bp, encoding a biologically active polyketide synthase of 6,879 amino acids of in this application (our seq ID #26). Factors affecting biosynthesis by *Xanthomonas albilineans* of albicidins antibiotics and phytotoxins are discussed in J. Appl. Microbiol. 85, 1023-1028. and Wall, M.K. & Birch, R.G. (1997). Genes for albicidin biosynthesis and resistance span at least 69 kb in the genome of *Xanthomonas albilineans*. Lett. Appl. Microbiol. 24, 256-260. A gene from *X. albilineans* strain Xa13, designed AlbF, which confers high level albicidin resistance in *Escherichia coli* and which encodes a putative albicidin efflux pump, was directly submitted to Genbank by Bostock and Birch (Accession n° AF403709).

SUMMARY OF THE INVENTION

The invention provides a novel antibiotic family, Albicidins, produced by three novel biosynthetic gene clusters (XALB1, XALB2, and XALB3) contained within a host cell DNA in which one strand comprises non-contiguously SEQ. ID No. 1, SEQ. ID No. 2 and SEQ ID No. 3, and the cell expresses the DNA to provide peptides including those named AlbI (SEQ ID No. 26) (encoded by SEQ ID No. 20), AlbII (SEQ ID No. 27) (encoded by SEQ ID No.21) , AlbIII (SEQ ID No. 28) (encoded by SEQ ID No. 22), AlbIV (SEQ ID No. 29) (encoded by SEQ ID No. 23), AlbVI (SEQ ID No. 31) (encoded by SEQ ID No. 18), AlbVII (SEQ ID No. 32) (encoded by SEQ ID No. 17), AlbVIII (SEQ ID No. 33) (encoded by SEQ ID No. 16), AlbIX (SEQ ID No. 34) (encoded by SEQ ID No. 15), AlbX (SEQ ID No. 35) (encoded by SEQ ID No. 10), AlbXI (SEQ ID No. 36) (encoded by SEQ ID No. 9), AlbXII (SEQ ID No. 37) (encoded by SEQ ID No. 8), AlbXIII (SEQ ID No. 38) (encoded by SEQ ID No. 7),

AlbXIV(SEQ ID No. 39) (encoded by SEQ ID No. 6), AlbXV (SEQ ID No. 40) (encoded by SEQ ID No. 5), AlbXVII (SEQ ID No. 42) (encoded by SEQ ID No. 11), AlbXVIII (SEQ ID No. 43) (encoded by SEQ ID No. 12), AlbXIX (SEQ ID No. 44) (encoded by SEQ ID No. 13) , AlbXX (SEQ ID No. 45) (encoded by SEQ ID No. 14), AlbXXI (SEQ ID No. 46) (encoded by SEQ ID No. 24), and AlbXXII (SEQ ID No. 47) (encoded by SEQ ID No. 25), that in turn interact within the host cell to produce one or more antibiotics as more fully illustrated in Figure 11. In one embodiment the invention comprises a plurality of isolated and purified DNA strands which comprise nucleotide sequences of the group consisting of SEQ ID No: 1 to SEQ. ID No. 25, each individual sequence, except the transposases AlbV (SEQ ID No. 30) (encoded by SEQ ID No. 19) and AlbXVI (SEQ ID No. 41) (encoded by SEQ ID No. 4) found in the XALB1 cluster, being necessary to the biosynthesis of the novel family of antibiotics, Albicidins. The invention also includes the peptides or proteins encoded by the genes of the biosynthetic complex expressed by the combination of DNA with a strand having sequences SEQ ID Nos. 1 to 3. Proteins are named with roman numerals and the prefix Alb from AlbI to Alb XXII have the amino acid sequences of SEQ ID Nos. 26 to 47 (not in Roman numeral order but in the order of placement of the genes within sequences SEQ ID Nos. 1 to 3 that express each protein). Expression of the peptides having the amino acid sequences of SEQ ID Nos. 26 to 29, 31 to 40 and 42 to 47, have been found to be all required for the successful biosynthesis of Albicidins. The invention provides a method for producing Albicidins comprising providing a modified host cell with a heterologous DNA Albicidin Biosynthetic Gene Cluster or set of genes defined as DNA operably comprising DNA sequences substantially similar to SEQ ID Nos. 1 to 3. Substantially the same means DNA having sufficient homology to provide expressed proteins that function to provide an antibiotic material having the structural components identified herein. Preferably a given sequence will have at least 70 percent homology to one of SEQ ID Nos. 1 to 3, preferably 85% homology and most preferably at least 95% homology. The method includes the steps consisting of, modifying the DNA of the host cell to comprise an operable expression system for maintaining the modified host cell under conditions supporting biosynthesis of Albicidins and isolation of Albicidins from the host cell or its environment. The invention further provides a method of production of a group of novel antibiotic materials utilizing at least three of the Sequences selected from the group consisting of DNA SEQ ID No. 1 to SEQ ID No. 25 (excluding transposases encoded by SEQ IDs No. 4 and 19) inclusive in combination with additional sequences to produce a modified Albicidin- like material.

More specifically, the invention provides DNA Sequences comprising at least about 68,498 base pairs more or less and including an about 55,839 bp region from the genome of *X.*

albilineans designated as XALB1 (SEQ ID. No. 1) and additional non contiguous regions having about 2,986 bp, XALB2 (SEQ ID. No. 2), and about 9,673 bp, XALB3 (SEQ ID. No. 3). These sequences were found to be required for biosynthesis of Albicidins. Homology analysis revealed the presence of (i) four large genes with a modular architecture characteristic of polyketide synthases (PKS) and nonribosomal peptide synthetases (NRPS) potentially involved in albicidin precursor biosynthesis; (ii) four smaller genes potentially involved in albicidin substrate biosynthesis (iii) four modifying genes; (iv) one enzyme activating gene, (v) two regulatory genes, (vi) one chaperone gene, (vii) two genes of unknown function; and (viii) two resistance genes. These are named and discussed more fully below. Together these genes allow the successful operation of the biosynthetic pathway when cloned into suitable host cells. Alignment of individual NRPS and PKS domains revealed an extraordinary biosynthetic apparatus believed to involve a *trans*-action of separate PKS and NRPS domains which could contribute to the production of multiple, structurally related albicidins by the same gene cluster. Furthermore, analysis of selectivity-conferring residues indicated that four NRPS modules of XALB1 specify an unusual substrate. Through the interaction of these genes the following methods are enabled: a) In an alternate embodiment the invention provides a method of producing a polyketide carrying para-aminobenzoic acid and/or carbamoyl benzoic acid by inserting at least one DNA Fragment that encodes a PKS protein into a cell and causing the cell to express the encoded PKS protein under conditions such that the PKS protein functions to produce a polyketide carrying either a para-aminobenzoic acid or a carbamoyl benzoic acid or both. b) Another alternate embodiment is a method of producing polyketide/peptides carrying para-aminobenzoic acid and/or carbamoyl benzoic acid by inserting at least one DNA Fragment that encodes a PKS protein into a cell and causing the cell to express the encoded PKS protein under conditions such that the PKS protein functions to produce a polyketide carrying either a para-aminobenzoic acid or a carbamoyl benzoic acid or both. Or c) In another alternate embodiment the invention provides a method of activating nonproteinogenic amino acids like paraminobenzoic acid and/or carbamoyl benzoic acid for incorporation into peptides or polyketides by inserting at least one DNA Fragment that encodes a PKS protein into a cell and causing the cell to express the encoded PKS protein under conditions such that the PKS protein functions to produce a polyketide carrying either a para-aminobenzoic acid or a carbamoyl benzoic acid or both.

There are three regions of the *X. albilineans* genome specifying albicidin production. The XALB2 and XALB3 regions each contain only one gene, both of which are required for post-translational activation and folding of albicidin PKS and NRPS enzymes. The XALB1, XALB2 and XALB3 gene clusters are characterized by an unusual hybrid NRPS-PKS system, indicating

that albicidin biosynthesis may provide an excellent model for investigating the biosynthesis of hybrid polyketide-polypeptide metabolites in bacteria. The availability of three genomic regions involved in albicidin production, XALB1 and XALB2 and XALB3, also offers the ability to express individually the enzymes of the albicidin family biosynthetic pathway including structural, resistance, secretory and regulatory elements, and to engineer overproduction of albicidin in mutated or modified host cells of the invention. The invention overcomes prior art limitations in albicidin production due to low yields of toxin production in *X. albilineans* and may also allow characterization of the chemical structure of albicidin as well as application of this potent inhibitor of procaryote DNA replication.

The invention results from a number of unpredictable results namely the number and complexity of the enzymes involved in biosynthesis. The discovery of the complete sequence required for biosynthesis of Albicidins is previously unreported. The invention provides for a novel process for production of molecule having a polyketide-polypeptide backbone and the formula $C_{40}H_{35}O_{15}N_6$, a molecular weight of 839, and the structural elements shown in Figure 11. The invention further includes (a) the Albicidin Family Biosynthetic Gene Cluster including (b) the structural and regulatory elements of the operons that encode c) the enzymes PKS-1, PKS-2, PKS-3, PKS-4, NRPS-1, NRPS-2, NRPS-3, NRPS-4, NRPS-5, NRPS-6 and NRPS-7 as well as (e) the proteins AlbI to AlbXXII, (f) the isolated enzymes, proteins, and active forms thereof, as well as mutants, fragments, and fusion proteins comprising any of the forgoing; (g) the uses of the enzymes or proteins encoded by the Albicidins Biosynthesis Gene Cluster or any one of its operons, (h) a host cell expressing one or more enzymes or proteins encoded by the Albicidin Family Biosynthetic Gene Cluster; (i) use of host cells having the Albicidins Biosynthesis Gene Cluster to produce an antibiotic; (j) methods of modifying the DNA sequences to produce members of a series of antibiotic compounds having structures related to Albicidins; (k) DNA sequences that encode the same proteins as any of SEQ. ID. Nos. 1 to 25 but differ in specific codons due to the multiplicity of codons that lead to expression of the same amino acid, (l) antibiotics produced by the process of expression of the Albicidin Family Biosynthetic Genes in a genetically modified host cell sustained in a culture medium and thereafter separation of the antibiotic from the host cell and culture medium, (m) an isolated and purified antibiotic produced by a process that includes at least three proteins coded by DNA sequences selected for the group consisting of SEQ. ID Nos. 1 to 25 in combination with additional enzymes that modify the product to provide a non-naturally occurring Albicidins like product having at least one of the useful properties reported for albicidin and (n) a process for producing an antibiotic that comprises modifying a host cell to enhance expression of the DNA of the Albicidin Family

Biosynthetic Gene Cluster by insertion of expression enhancing DNA into the genome of a *Xanthomonas albilineans* strain in a position operative to enhance expression of the enzymes of the Albicidin Family Biosynthetic Gene Cluster, culturing the modified host cell to produce an antibiotic and isolating the antibiotic. The products and methods described above have utility as proteins or as nucleic acids as the case may be, including such uses sources of pyrimidine or purine bases or amino acids, or as animal food supplements and the like, as well as the more important uses to provide antibiotics, plant disease treatment methods, genetically modified disease resistant plants, phytotoxins and the like.

BRIEF DESCRIPTION OF THE DRAWINGS

Figure 1 is a Physical Map and genetic organization of the DNA Region containing the major gene cluster XALB1 involved in the biosynthesis of Albicidins.

Figure 2 is an illustration of the organization of the four PKS modules and the seven NRPS modules identified in cluster XALB1 and comparison with the organization of the prior art material XabB.

Figure 3 shows the conserved sequence motifs in O-methyltransferases and C-methyltransferases involved in antibiotic biosynthesis in bacteria and in AlbII.

Figure 4 shows the conserved sequence motifs in O-methyltransferases and in different tcmP-like hypothetical proteins and AlbVI.

Figure 5 is an illustration of the alignment of the primary sequences between the conserved motifs A4 and A5 of Alb NPRSs and PKS-4 in *Xanthomonas albilineans* with the corresponding sequences of GrsA (Phe) accession number:P14687 and Blm NRPS-2 (β-Ala) accession number AF210249.

Figure 6 shows Rho-independent transcription terminators identified in the intergenic regions of XALB1 and XALB3 clusters.

Figure 7A shows sequences identified as a putative bidirectional promoter between albX and albXVII in XALB1 for transcriptional control of operons 3 and 4.

Figure 7B shows sequences identified as a putative unidirectional promoter upstream from *albXIX* for transcriptional control of operon 5 if *albXVIII* is not expressed.

Figure 8 is a physical map and genetic organization of the DNA region containing the gene clusters XALB2 and XALB3 involved in albicidin production.

Figure 9A is linear model 1 leading to the biosynthesis of only one polyketide-polypeptide albicidin backbone.

Figure 9B is linear model 2 leading to the biosynthesis of four different polyketide-polypeptide

backbone.

Figure 10A is an alignment of the conserved motifs in AT domains from RifA-1 , -2 , -3 , RifB-1, RifE-1 (Rifamycin PKSs, August *et al.*, 1998) and BlmVIII (Bleomycin PKS; Du *et al.*,2000).

Figure 10B is a comparison of AlbXIII, FenF (a malonyl-CoA transacylase located upstream from *mycA*, Duitman *et al.*, 1999) and LipA (a lipase; Valdez *et al.*, 1999).

Figure 11A is a proposed model for biosynthesis of albicidin, including putative substrates of PKS and NRPS modules.

Figure 11B shows the proposed compositions and structures of albicidins.

DETAILED DESCRIPTION OF THE INVENTION

The invention results from the DNA sequencing of the complete major gene cluster XALB1, as well as the noncontiguous fragments XALB2 and XALB3. XALB1 is present in the two overlapping DNA inserts of clones pALB540 and pALB571. Reading frame analysis and homology analyses allow one to predict the genetic organization of XALB1 and to assign a function to the genes potentially required for albicidin production. Based on the alignment of the different PKS and/or NRPS enzymes encoded by XALB1 we proposed a model for the albicidin backbone biosynthesis. However the invention disclosed herein does not depend upon the accuracy of the proposed model. The invention includes the successful cloning and DNA sequencing of the second region of the genome (XALB2) involved in albicidin production and mutated in mutant AM37.

The invention includes the characterization of the third region of the genome (XALB3) involved in albicidin production present in clone pALB639. These results allowed the possibility to characterize all enzymes of the albicidin biosynthesis pathway including structural, resistance and regulatory elements and to engineer overproduction of albicidin.

EXAMPLE 1: Materials and methods

Bacterial strains and plasmids. The source of bacterial strains and their relevant characteristics are described in Table 1.

Media, antibiotics, and culture conditions. *X. albilineans* strains were routinely cultured on modified Wilbrink's (MW) medium at 30°C without benomyl (Rott *et al.*, 1994). For long-term storage, highly turbid distilled water suspensions of *X. albilineans* were supplemented with

glycerol to 15% (vol/vol) and frozen at –80°C. For *X. albilineans*, MW medium was supplemented with the following antibiotics as required at the concentrations indicated: kanamycin, 10 or 25 µg/ml; and rifampicin, 50 µg/ml. *E. coli* strains were grown on Luria-Bertani (LB) agar or in LB broth at 37°C and were maintained and stored according to standard protocols (Sambrook *et al.*, 1989). For *E. coli*, LB medium was supplemented with the following antibiotics as required at the concentrations indicated: kanamycin, 50 µg/ml; ampicillin, 50 µg/ml.

Bacterial conjugation. DNA transfer between *E. coli* donor (DH5αMCR/pAlb389 or pAC389.1, Table 1) and rifampicin-resistant *X. albilineans* recipients (*X.* strains AM10, AM12, AM13, AM36 and AM37, Table 1) was accomplished by triparental conjugation with plasmid pRK2073 as the helper as described previously (Rott *et al.*, 1996).

Table 1 : Bacterial strains and plasmids used in this study

	Relevant characteristics[a]	Reference or source
Strains		
E. coli		
DH5α	F-*f*80d*lac*ZΔM15 Δ(*lac*ZYA-*arg*F)U169 *deo*R *recA*1 *endA*1 *hsdR17*(r_k^- m_k^+) supE44 thi-1 *gyrA*96 *relA*1	Gibco-BRL
DH5α MCR	DH5α *mcrA mcrBC mrr*	"
X. albilineans		
Xa23	Wild type from sugarcane (Florida)	Rott *et al.*, 1996
Xa23R1	Spontaneous Rif^r derivative of Xa23	"
15 AM strains	Xa23R1::Tn*5-gusA*, Km^r, Rif^r, Tox$^-$	"
Plasmids		
PBR325	Tc^r, Ap^r, Cm^r	Gibco-BRL
pBCKS (+)	Cm^r	Stratagene
pBluescript II KS (+)	Ap^r	"
PRK2073	PRK2013 derivative, Km^s (*npt*::Tn*7*), Sp^r, Tra$^+$, helper plasmid	Leong *et al* , 1982
pUFR043	IncW Mob$^+$ LacZα, Gm^r, Km^r, Cos	De Feyter and Gabriel, 1991
pAlb540	47 kb insert from Xa23R1 in pUFR043, Gm^r, Km^r	Rott *et al.*, 1996
pAlb571	36.8 kb insert from Xa23R1 in pUFR043, Gm^r, Km^r	"
PAlb639	36 kb insert from Xa23R1 in pUFR043, Gm^r, Km^r	"

pAM15.1	24 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM15 in pBR325, Km^r, Tc^r, Ap^r, Cm^r	"
pAM40.2	11 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM40 in pBR325, Km^r, Tc^r, Ap^r, Cm^r	"
pAM45.1	12 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM45 in pBR325, Km^r, Tc^r, Ap^r, Cm^r	"
pAM12.1	13 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM12 in pBR325, Km^r, Tc^r, Ap^r, Cm^r	"
PAM36.2	9 kb*Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM36 in pBR325, Km^r, Tc^r, Ap^r, Cm^r	"
pAlb389	37 kb insert from Xa23R1 in pUFR043, Gm^r, Km^r	This study
pAC389.1	2.9 kb insert from Xa23R1 in pUFR043, Gm^r, Km^r	"
PAlb639A	9.4 kb insert from Xa23R1 in pUFR043, Gm^r, Km^r	"
PEV639	2.6 kb *Sal* I insert from Xa23R1 in pUFR043, Gm^r, Km^r	"
pBC/A'	7.5 kb *Kpn* I fragment carrying a part of fragment A from pAlb571 in pBCKS (+), Cm^r	"
pBC/AF	15.2 kb *Eco*R I fragment carrying fragments A and F from pALB540 in pBCKS (+), Cm^r	"
pBC/B	11.0 kb *Kpn* I fragment B from pAlb571 in pBCKS (+), Cm^r	"
pBC/C	6.0 kb *Kpn* I fragment C from pAlb571 in pBCKS (+), Cm^r	"
pBC/E	2.8 kb *Kpn* I fragment E from pAlb571 in pBCKS (+), Cm^r	"
pBC/F	2.5 kb *Kpn* I-*Eco*R I fragment F from pAlb571 in pBCKS (+), Cm^r	"
pBC/G	1.9 kb *Eco*R I fragment G from pAlb571 in pBCKS (+), Cm^r	"
pBC/I	1.4 kb *Kpn* I-*Eco*R I fragment I from pAlb571 in pBCKS (+), Cm^r	"
pBC/J	0.6 kb *Eco*R I fragment J from pALB540 in pBCKS (+), Cm^r	"
pBC/K	4.7 kb *Eco*R I fragment K from pALB540 in pBCKS (+), Cm^r	"
pBC/L	0.4 kb *Eco*R I fragment L from pALB540 in pBCKS (+), Cm^r	"
pBC/N	7.7 kb *Eco*R I fragment N from pALB540 in pBCKS (+), Cm^r	"
pUFR043/D'	2.2 kb *Eco*R I–*Sau*3A I fragment carrying a part of fragment D from pAlb571 in pUFR043	"
pAM1	5 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM1 in pBluescript II KS (+), Km^r, Ap^r	"
pAM4	12 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM4 in pBluescript II KS (+), Km^r, Ap^r	"
pAM7	6 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM7 in pBluescript II KS (+), Km^r, Ap^r	"
pAM10	7 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of	"

	mutant AM10 in pBluescript II KS (+), Km^r, Ap^r	
pAM29	10 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM29 in pBluescript II KS (+), Km^r, Ap^r	"
pAM37	6 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM37 in pBR325, Km^r, Tc^r, Ap^r, Cm^r	"
pAM52	5 kb *Eco*R I fragment carrying Tn*5* and flanking sequences of mutant AM52 in pBluescript II KS (+), Km^r, Ap^r	"
DNA Fragment		
PR37	1.1 kb *Hind* III-*Hind* III from pAM37	"

[a] Ap^r, Cm^r, Gm^r, Km^r, Rif^r, Sp^r, Tc^r: resistant to ampicilin, chloramphenicol, gentamycin, kanamycin, rifampicin, spectinomycin, tetracycline, respectively. Tox-, deficient in albicidin production. Tn*5-gusA*, Tn*5-uidA1* Km^r Tc^r, forms transcriptional fusions.

Assay of albicidin production. Albicidin production was tested by a microbiological assay as described previously (Rott *et al.*, 1996). Rifampicin and kanamycin exconjugants were spotted with sterile toothpicks (2-mm-diameter spots) onto plates of SPA medium (2% sucrose, 0.5% peptone, 1.5% agar) and incubated at 28°C for 2-5 days. The plates were then overlaid with a mixture of *E. coli* DH5α (10^7 cells in 2 ml of distilled water) plus 2 ml of molten 1.5% (wt/vol) Noble agar (Difco) at ca. 65°C and examined for inhibition zones after 24 h at 37°C.

Nucleic acid manipulations. Standard molecular techniques were used to manipulate DNA (Sambrook *et al.*, 1989) except for total genomic DNA preparation. Total genomic DNA for southern blot hybridization was prepared as described by Gabriel and De Feyter (1992).

PCR Conditions. PCR amplifications were performed in an automated thermal cycler PTC-100™ (MJ Research, Inc). The 25 µl PCR reaction mix consisted of 100 ng of genomic DNA or 1 ng of plasmid DNA, 2.5 µl of 10X PCR buffer without MgCl2 (Eurobio), 80 µM dNTP mix, 2.5 units of EUROBIOTAQII® (Eurobio), 25 pmoles of each primer, 2.0 mM $MgCl_2$ (Eurobio) and sterilized distilled water to final volume. The PCR program was 95°C for 2 min, 25 cycles at 94°C for 1 min, Tm for 1 min and 72°C for 1 min, with a final 72°C extension for 5 min. Tm temperature was determined for each couple of primers and varied between 55°C and 60°C. A 5µl aliquot of each amplified product was analyzed by electrophoresis through a 1% agarose gel. For sequencing, PCR products were cloned with the pGEM®-T Easy Vector System (Promega).

Oligonucleotide synthesis. Oligonucleotides were purchased from Genome Express (Grenoble or Montreuil, France).

DNA sequencing. Automated DNA sequencing was carried out on double-stranded DNA by the dideoxynucleotide chain termination (Sanger *et al.*, 1977) using a Dye Terminator Cycle Sequencing kit and an ABI Perkin-Elmer sequencer according to the manufacturer's procedure. Both DNA strands were sequenced with universal primers or with internal primers (20mers). This service was provided by Genome Express (Grenoble, France). Computer-aided sequence analyses were carried out using Sequence Navigator™ (Applied Biosystems, Inc) and SeqMan (DNASTAR Inc.) programs.

Sequence analysis. Nucleotide sequences were translated in all six reading frames using EditSeq (DNASTAR Inc.). Potential products of ORFs longer than 100 b were compared to protein data bases by the PSI-BLAST program (Swiss-Prot and Genbank) on the NCBI site (http://www.ncbi.nlm.nih.gov/) using Altschul program (Altschul *et al.*, 1997). The TERMINATOR program of the Genetics Computer Group was used to identify putative Rho-independent transcription terminators.

Procedures

EXAMPLE 2: Sequencing of the double strand region of 55,839 bp from *X. albilineans* containing XALB1 SEQ ID NO. 1

In Figure 1 is presented a physical map and genetic organization of XALB1. In the figure, E and K are restriction endonuclease sites for *Eco*RI and *Kpn*I, respectively. Rectangular boxes represent DNA fragments labeled A through N. The numbers below each rectangular box are the number of Tn*5-gus* insertion sites previously located in each DNA fragment (Rott *et al.*, 1996). The DNA inserts carried by plasmids pALB571 and pALB540 are represented by bold bars above the physical map. The location and direction of putative orfs identified in the XALB1 gene cluster are shown by arrows. Precise positions and proposed functions for individual orfs are summarized in tables 2 and 3, respectively. Position of insertional sites of eight albicidin-defective mutants determinated by sequencing are indicated by vertical arrows. The location and direction of putative ORFS identified in the XALB1 gene cluster are shown by arrow shapes. These twenty putative ORFs are potentially organized in four or five operons, as

indicated at the bottom of the figure. Patterns indicate NRPS and PKS genes (diagonal crosshatch), methyl transferase and esterase genes (hollow rectangles), carbamoyl transferase gene (fine crosshatch), benzoate-derived products biosynthesis genes (white), regulatory genes (vertical lined), resistance genes (diagonal lines) and other genes with function of unknown significance to albicidin production (black), and three insertional sites of eight albicidin-defective mutants determinated by sequencing are indicated by vertical arrows. Dotted regions in the physical map and in ORFs represent the two internal duplicated DNA regions of XALB1.

The sequence illustrated in Figure 1 was generated as follows. The sources of DNA are set out in Table 1. DNA fragments F, E, B, C, I, and G, generated by the digestion of cosmid pALB571 (Rott *et al.*, 1996) with *Eco*RI and/or *Kpn*I, were subcloned into pBCKS (+) and were sequenced from the resulting subclones, pBC/F, pBC/E, pBC/B, pBC/C, pBC/I and pBC/G. DNA fragment D' which corresponds to the part of fragment D present in cosmid pALB571 was sequenced from plasmid pUFR043/D' obtained following self ligation of the complete *Eco*RI digested cosmid pALB571. DNA fragment H was sequenced from pAM45.1 (Rott *et al.*, 1996), obtained following cloning into vector pBR325 of the 12kb *Eco*RI fragment carrying Tn*5* and flanking sequences from mutant strain XaAM45. DNA fragment A' contains the part of fragment A present in cosmid pALB571 and was subcloned into vector pBCKS (+) and the resulting plasmid pBC/A' was used for sequencing. The presence of a large internal duplication made alignment of sequence data obtained from pBC/A' difficult. This difficulty was resolved using sequence data obtained from an additional plasmid, pAM4, obtained following cloning into vector pBluescript II KS (+) of the 12kb *Eco*RI fragment carrying Tn*5* and flanking sequences from mutant strain XaAM4, which contains only one copy of the large internal duplication. Sequence data from pBC/A' were used to determine the first 1542 bp of fragment A' between nucleotides C-19001 and G-20543. Sequence data from pAM4 and pBC/A' were used to determine the last 4823bp of fragment A' between nucleotides G-21653 and G-26477. The overlapping region between nucleotides G-20469 and C-22159 was amplified by PCR from cosmid pALB571 using primers contig13-1160 (5'gcgtaccgttgtccagtagg3') SEQ ID NO. 48 and pAM4-14 (5'gctggaaaccgagaatctga3') SEQ ID NO. 49, and was sequenced. Resulting sequence data were used to complete

sequencing of DNA fragment A'. The junctions A/F, F/H, H/E, E/B, B/C, C/I, I/G, G/D between corresponding DNA fragments were sequenced directly from cosmid pALB571. EcoRI DNA fragment containing fragments A and F was subcloned from pALB540 into pBCKS (+), and the resulting plasmid pBC/AF was used to determine the part of DNA fragment A which was not present in cosmid pALB571 between nucleotides G-13682 and G-19001. EcoRI DNA fragments J, K, L, N were subcloned from pALB540 into pBCKS (+) and were sequenced from resulting plasmid pBC/J, pBC/K, pBC/L, and pBC/N. The junctions L/K, K/J and J/A between corresponding DNA fragments were sequenced directly from cosmid pALB540. DNA region between nucleotides G-7517 and T-8721 was amplified by PCR from cosmid pALB540 using primers E114 (5'gacacgatcagccgctagga3') SEQ ID NO. 50 and EI4-380 (5'accagcagttgggccagcct3') SEQ ID NO. 51 and was sequenced. Resulting sequence data were used to determine the sequence of fragment M and of junctions N/M and M/L. The nucleotide sequence of 55,839 bp containing the entire major gene cluster involved in Albicidin production was sequenced on both strands.

EXAMPLE 3: Analysis of the large internal duplications in the DNA sequence of XALB1

The sequence of the 55,839 bp genomic region (SEQ ID NO. 1) contains two large internal duplications as shown by the dotted regions in the physical map of Figure 1. A direct duplication of 1736 bp was located in DNA fragment A between nucleotides G-19904 and G-21639 and between nucleotides G-23057 and G-24792. Another direct duplication of a 2727 bp was found in DNA fragments B and C between nucleotides C-40410 and G-43136 and between nucleotides C-46644 and G-49370. Comparison of the two copies of each duplication revealed that the two copies of the 1736 bp duplication are identical except for one nucleotide at position 21058, and that the two copies of the 2727 bp duplication are 98.8% identical and differ by 30 nucleotides.

EXAMPLE 4: Comparison of XALB1 with the *xabB Eco*RI fragment

Comparison of the DNA sequence of the 55,839 bp genomic region described in this study with the partial DNA sequence of 16,511 bp of the same region in Huang et al.,

2001 (described by Huang et al. as an *Eco*RI fragment including full length xabB from *X. albilineans* strain Xa13 [GenBank accession N° AF239749]), revealed that the DNA sequence from strain Xa13 over 16,511 bp is identical to the sequence from strain Xa23R1, described herein, with the following exceptions: 1) five nucleotides are different at positions 42963, 42972, 42980, 43014 and 43071 of the XALB1 sequence, and 2) nucleotides from positions 43137 to 49370 are missing (internal to *albI*; refer Fig. 1). Analysis of genomic DNA of seven strains isolated from different countries (Australia, Reunion Island, Kenya, Zimbabwe and USA), digested by *Kpn*I and hybridized with the pBC/C plasmid (Table 1) labeled with ^{32}P, revealed that two DNA fragments corresponding to the XALB1 fragments B and C were present in all strains (data not shown). This result indicated that all studied strains contain *albI* and not *xabB* because in *albI* the pBC/C plasmid probe hybridizes with the large internal duplication present in both DNA fragments B and C (Figure 1). Based on this observation we postulated that the DNA sequence of XabB reported as full length by Birch in PCT WO 02/24736 A1 (Their seq. ID#1) appears to be incomplete and missing 6,234 bp of DNA sequence encoding 2,078 amino acids.

EXAMPLE 5: Reading frame analysis in XALB1

Analysis of the 55,839 bp double strand region for coding sequences revealed the presence of 20 open reading frames (ORFs) designated *albI* to *albXX* (Table 2 below) which are distributed in four groups of genes according to their position and their orientation in the XALB1 cluster (Figure 1). Genes of each group may form part of the same operon as judged by their overlapping stop and start codons, or by the relatively short intergenic region which varies from 5 to 274 nucleotides. The 20 ORFs appear to be organized in four operons: operon 1 formed by *albI - albIV*; operon 2 by *albV - albIX*; operon 3 by *albX - albXVI*; operon 4 by *albXVII - albXX*. The majority of *alb* ORFs are initiated with an ATG codon, except *albI* and *albXVII* which are initiated with a TTG codon, and *albIV* and *albVI* which are initiated with a GTG start codon. In seven ORFs of XALB1, start codons are preceded by the consensus sequence GAGG which may correspond to the ribosome binding site. Other ORFs are preceded by a less conserved sequence which contain at least three nucleotides A or G and which may serve as a weak

ribosome binding site.

EXAMPLE 6: Sequencing of the Tn*5* insertional site of eight tox⁻ mutants previously located in XALB1

Eight of the 45 *X. albilineans* Tox⁻ mutants complemented by cosmid pALB540 and/or cosmid pALB571 and previously described (Rott *et al.*, 1996) were further analyzed. All eight mutants contain a single Tn*5* insertion and correspond to the following *X. albilineans* strains: XaAM7, XaAM15, XaAM45, and XaAM52 which are complemented by pALB571 but not by pALB540; XaAM4, XaAM29 and XaAM40 which are complemented by both cosmids; and XaAM1 which is complemented by pALB540 but not by pALB571. The Tn*5* insertional site of each Tox⁻ mutant was sequenced from plasmids obtained following cloning in pBR325 or in pBluescript II KS (+) of the EcoRI fragments carrying Tn*5* and flanking sequence using the sequencing primer GUSN (5'tgcccacaggccgtcgagt3') SEQ ID No. 52 that annealed 135 bp downstream from the insertional sequence IS50L of Tn*5*-*gus*A. The sequence of the Tn*5* insertional site was compared with the 55,839 bp sequence containing XALB1 in order to determine the *alb* gene disrupted in each Tox⁻ mutant. *albI* is disrupted by the Tn*5* insertion in XaAM15 and XaAM45 at position 33443 and 34229, respectively (Figure 1). *albIV* is disrupted by the Tn*5* insertion in XaAM7 and XaAM52 at position 53704 and 53915, respectively. *albIX* is disrupted by the Tn*5* insertion in XaAM4, XaAM29 and XaAM40 at position 21653, 23444 and 24376, respectively. *alb XI* is disrupted by the Tn*5* insertion in XaAM1 at position 13301. These results are in accordance with the previous characterization of Tox⁻ mutants using Southern blot hybridization (Rott *et al.*, 1996), except for XaAM1. The Tn*5*-*gusA* insertion site of XaAM1 was previously located in DNA fragment A (Rott *et al.*, 1996) but results of this study showed that this site is located in DNA fragment J (Figure 1).

Table 2: Analysis of putative translational signals and location of all putative orfs identified in the XALB1 gene cluster

Intergenic spacing between consecutive orfs in each putative operon	Orf	Potential RBS[a] (distance from start codon)	Start codon (position)	Stop codon (position)
Operon 1 (strand +)				
	albI	GAGGG (5 b)	TTG (30166)	TAG (50805)
45 b	*albII*	GAGGG (5 b)	ATG (50851)	TAA (51882)
ATG overlaps TAA	*albIII*	GAGGG (7 b)	ATG (51882)	TGA (52385)
GTG overlaps TGA	*albIV*	GAGG (7 b)	GTG (52382)	TAA (55207)
Operon 2 (strand -)				
	albV	GGAGG (8 b)	ATG (29929)	TAA (29210)
87 b	*albVI*	AAGG (4 b)	GTG (29122)	TGA (28262)
61 b	*albVII*	GAG (4 b)	ATG (28200)	TAG (25903)
7 b	*albVIII*	AGGTG (4 b)	ATG (25895)	TAA (24903)
20 b	*albIX*	GGTG (3 b)	ATG (24882)	TGA (19003)
Operon 3 (strand -)				
	albX	GGGGG (8 b)	ATG (14497)	TGA (14246)
81 b	*albXI*	AGGAAA (6 b)	ATG (14164)	TGA (13217)
5 b	*albXII*	GGCCTGA (5 b)	ATG (13211)	TAA (11856)
36 b	*albXIII*	GGGG (3 b)	ATG (11819)	TAA (10866)

12 b	*albXIV*	GGAG (8 b)	ATG (10853)	TAG (9363)
41 b	*albXV*	GGAA (6 b)	ATG (9321)	TAG (7567)
208 b	*albXVI*	GGAGG (4 b)	ATG (7358)	TAG (7092)
Operon 4 (strand +)				
	albXVII	GGGAGG (5 b)	TTG (14909)	TGA (17059)
274 b	*albXVIII*	GCTCAG (8 b)	ATG (17334)	TGA (17747)
Overlap (17 b)	*albXIX*	AGG (9 b)	ATG (17728)	TGA (18330)
41 b	*albXX*	GCAA (8 b)	ATG (18372)	TAG 18980)

[a]: Ribosomal Binding Site

EXAMPLE 7: Homology analysis of proteins potentially encoded by XALB1

Preliminary functional assignments of individual ORFs were made by comparison of the deduced gene products with proteins of known functions in the Genbank database. The results are set out in Table 3 below. Among the ORFs identified from the sequenced XALB1 gene cluster, we found (i) four genes, *albI* SEQ ID No. 20, *albIV* SEQ ID No. *23, albVII* SEQ ID No. 17 and *albIX* SEQ ID No. 15, encoding PKS and/or NRPS modules; (ii) one carbamoyl transferase gene, *albXV* SEQ ID No. 5; (iii) two esterase genes, *albXI* SEQ ID No. 9 and *albXIII* SEQ ID No. 7; (iv) two methyltransferase genes, *albII* SEQ ID No. 21 and *albVI* SEQ ID No. 18; (v) two benzoate-derived products biosynthesis genes, *albXVII* SEQ ID No. 11 and *albXX* SEQ ID No.14; (vi) two putative albicidin biosynthesis regulatory genes, *albIII* SEQ ID No. 22 and *albVIII* SEQ ID No. 16; (vii) two putative albicidin resistance genes, *albXIV* SEQ ID No. 6 and *albXIX* SEQ ID No. 13; and (viii) two additional ORFs encoding proteins similar to transposition proteins, *albV* SEQ ID No. 19 and *albXVI* SEQ ID No. 4. No known function was found in the database for *albX* SEQ ID No. 10 and *albXII* SEQ ID No. 8. The potential product of *albXVIII* SEQ ID No. 12

appeared to be a truncation of an enzyme with strong similarity to 4-amino-4-deoxychorismate lyase and branched-chain amino acid aminotransferase. Since the gene encoding the predicted product is roughly half the length of other such lyase or aminotransferase genes, *albXVIII* may be the result of a recombination event and may be non functional.

Table 3: Deduced functions of the ORFs in the major albicidin biosynthetic cluster X-ALB1

Orf	Number of amino acids	Sequence homolog [a]	Proposed function[a,c]
Operon 1			
albI	6879	XabB (AAK15074)	Polyketide- peptide synthase PKS modules PKS domains PKS-1 AL ACP1 PKS-2 KS1 KR ACP2 ACP3 PKS-3 KS2 PCP1 NRPS modules NRPS domains NRPS-1 C A PCP2 NRPS-2 C A PCP3 NRPS-3 C A PCP4 NRPS-4 C
albII	343	XabC (AAK15075)	*C*-methyltransferase
albIII	167	ComAB (CAA71583)	Activator of *alb* genes transcription
albIV	941	MycA (T44806) WbpG (E83253)	Peptide synthase NRPS module NRPS domains NRPS-5 A PCP5
Operon 2			
albV	239	Thp (AAK15074)	No function (transposition)
albVI	286	TcmP (AAA67510)	*O*-methyltransferase
albVII	765	HbaA (A58538)	4-hydroxybenzoate CoA ligase
albVIII	330	SyrP (AAB63253)	Regulation
albIX	1959	DhbF (CAB04779)	Peptide synthase NRPS modules NRPS domains

			NRPS-6 A PCP6 NRPS-7 C A PCP7
Operon 3			
albX	83	MbtH (O05821)	Unknown
albXI	315	SyrC (U25130)	Thioesterase
albXII	451	BoxB (AAK006000.1)	Unknown
albXIII	317	hp[d] (AAK25001)	Esterase
albXIV	496	ActII-2 (p46105)	Albicidin transporter
albXV	584	hp[d] (08390)	Carbamoyl transferase
AlbXVI	88	OrfA (AAC03166)	No function (transposition)
Operon 4			
albXVII	716	PabAB (CAC22117)	Para-amino benzoate synthase
Operon 5			
albXVIII	137	ADCL (AAG06352)	No function (not functional)
albXIX	200	McbG (P05530)	Immunity against albicidin
albXX	202	UbiC (S25660)	4-hydroxybenzoate synthetase

[a]Protein accession numbers in Genbank are given in parentheses.

[b]NRPS and PKS domains are abbreviated as follows: A, adenylation; ACP, acyl carrier protein, AL, acyl CoA ligase; C, condensation; KR, ketoreductase; KS, ketoacyl synthase; PCP, peptidyl carrier protein

[c]Underlined domains are likely inactive due to the lack of highly conserved motifs.

[d]hypothetical protein

EXAMPLE 8: The *alb* PKS and/or NRPS genes

The potential product of *albI*, designated AlbI SEQ ID No. 20, is a protein of 6879 aa with a predicted size of 755.9 kDa. This protein is very similar to the potential product of the *xabB* gene from *X. albilineans* strain Xa13 from Australia (Huang *et al.*, 2001), but it differs in length and size (See Table 4 below). XabB is a protein of 4801 aa with a predicted size of 525.7 kDa. Comparison of AlbI with XabB revealed that the N-terminal regions from Met-1 to Ile-4325 of both proteins are identical except for five amino-acids which are Tyr-3941, Pro-3952, Ala-4054, Ala-4271 and Gln-4284 in AlbI and His-3941, Ala-3952, Val-4054, Val-4271 and Glu-4284 in XabB. The same comparison revealed that the AlbI C-terminal region from Arg-6404 to the stop codon is 100% identical to the XabB C-terminal region from Arg-4326 to the stop codon.

The N-terminal region (from Met-1 to Asp-3235) of AlbI is 100% identical to the corresponding region in XabB which was previously described as similar to many microbial modular PKS (Huang *et al.*, 2001). This PKS region may be divided into three modules (Figure 2). Abbreviations used in the Figure are: A, adenylation; ACP, acyl carrier protein; AL, acyl-CoA ligase; C, condensation; KR, -ketoacyl reductase; KS, -ketoacyl synthase; NRPS, nonribosomal peptide synthase; PCP, peptidyl carrier protein; PKS, polyketide synthase; TE, thioesterase; HBCL, 4-hydroxybenzoate-CoA ligase. The question mark in the NRPS-2 domain indicates that this A domain is incomplete. The first module designated PKS-1 contains acyl-CoA ligase (AL) and acyl carrier protein (ACP1) domains. The second module designated PKS-2 contains β-ketoacyl synthase (KS1) and β-ketoacyl reductase (KR) domains followed by two consecutive ACP domains (ACP2 and ACP3). The third module designated PKS-3 contains a KS domain (KS2) followed by a PCP domain (PCP1). Apart their very high similarity with XabB, these three PKS modules exhibited the highest degree of overall similarity with polyketide synthases SafB and PksM from *Myxococcus xanthus* and *Bacillus subtilis*, respectively (Table 4). The motifs characteristic of these domains are 100% identical to those of XabB which were previously aligned with those from other organisms (Huang *et al.*, 2001). The AL domain contains the conserved adenylation core sequence (SGSSG) and the ATPase motif (TGD). The three ACP domains contain a 4'-phosphopantetheinyl-binding cofactor box GxDS(IL), except that A replaced G in ACP1. Both KS domains contain motif GPxxxxxxxCSxSL around the active site Cys, and two His residues downstream from the active site Cys, in motifs characteristic of these enzymes. The KR domain contains the NAD(P)H-binding site GGxGxLG.

The PKS part of AlbI is linked by the PCP1 domain to the four apparent nonribosomal peptide synthase modules designated NRPS-1, NRPS-2, NRPS-3 and NRPS-4 (Figure 2). NRPS-1, NRPS-2 and NRPS-3 modules display the ordered condensation, adenylation (A) and PCP domains typical of such enzymes (Marahiel *et al.*, 1997), and NRPS-4 consists of an extra C domain which may correspond to an incomplete NRPS module. Known conserved sequences, characteristic of the domains commonly found in peptide synthases (Marahiel *et al.*, 1997), were compared to those from NRPS-1, NRPS-2, NRPS-3 and NRPS-4 (Tables 5, 6 and 7). Sequences characteristic of C, A, or PCP domains are conserved in these four NRPS, except in A domain of NRPS-2 module, suggesting that this latter A domain may be not functional. Comparison of the four NRPS modules among themselves revealed that NRPS-2, NRPS-3 and NRPS-4 modules were 30.7%, 94.4% and 47.5% similar to NRPS-1 module, respectively. Comparison with XabB revealed NRPS-2 and NRPS-3 modules were not present

in XabB which contains only NRPS-1 and NRPS-4 modules (Figure 2). The dotted box in Figure 2 corresponds to the apparent deletion of the NRPS-2 and NRPS-3 modules in XabB as compared to AlbI. Apart their very high similarity with XabB, Alb I NRPS modules exhibited the highest degree of overall similarity with non-ribosomal peptide synthases NosA and NosC from *Nostoc* sp..

albIV potentially encodes a protein of 941 aa (AlbIV) with a predicted size of 104.8 kDa. AlbIV is similar to several non-ribosomal peptide synthases such as the BA3 peptide synthase involved in bacitracin biosynthesis in *Bacillus licheniformis* (Table 4). AlbIV forms one NRPS module designated NRPS-5 that contains only an A domain and a PCP domain (Figure 2). Sequences characteristic of the domains A and PCP commonly found in peptide synthases (Marahiel *et al.*, 1997) are conserved in AlbIV (Tables 6 and 7). However the A domain present in AlbIV differs from A domains commonly found in peptide synthases: conserved sequences corresponding to cores A8 and A9 in AlbIV are separated by a very long peptide sequence of 390 amino-acids. This additional peptide sequence exhibits a significative similarity with the protein WbpG of 377 amino acids involved in the biosynthesis of a lipopolysaccharide in *Pseudomonas aeruginosa* (Table 4).

albVII potentially encodes a protein of 765 aa (AlbVII) with a predicted size of 83.0 kDa similar to the 4-hydroxybenzoate-CoA ligase from several bacteria and the closest protein (HbaA) was from *Rhodopseudomonas palustris* (Table 4). High similarity between AlbVII and HbaA suggests that AlbVII is a 4-hydroxybenzoate-CoA ligase and constitutes a fourth PKS module designed PKS-4. The size of HbaA is smaller (539 aa) and the similarity between the two proteins starts only at the residue 277 of AlbVII and at the residue 28 of HbaA. Comparison of AlbVII sequence located upstream from residue 277 produced no significant alignment. AlbVII, like 4-hydroxybenzoate-CoA ligases, contains some conserved sequences characteristic of the A domain commonly found in peptide synthases (Table 6).

albIX potentially encodes a protein of 1959 aa (AlbIX) with a predicted size of 218.4 kDa similar to non-ribosomal peptide synthases. Known conserved sequences, characteristic of the domains commonly found in peptide synthases (Marahiel *et al.*, 1997), were compared with those from AlbIX which forms two NRPS modules designated NRPS-6 and NRPS-7 (Tables 5, 6 and 7). NRPS-6 contains only one A and one PCP domain. NRPS-7 contains the three domains characteristic of NRPS modules (A-C-PCP) followed by a TE domain (Figure 2). Apart their very high similarity with XabB, NRPS-6 and NRPS-7 modules exhibited the highest degree of overall similarity and identity with non-ribosomal peptide synthases DhbF from *B. subtilis* and NosA from *Nostoc* sp. (Table 4).

Table 4 : Summary of results obtained from BLAST analyses.

Putative Alb protein	No. of aa residues	Protein homolog	Origin	Genbank accession #	Score	Expect	Identities	Positives	Gaps
AlbI	6879								
PKS-1		XabB (4801 aa) SafB (1770 aa)	*Xanthomonas albilineans* *Myxococcus xanthus*	AAK15074 AAC44128	1352 bits (3498) 231 bits (589)	0.0 2e-59	730/730 (100%) 175/532 (32%)	730/730 (100%) 269/532 (49%)	- 23/532 (4%)
PKS-2		XabB (4801 aa) PksM (4273 aa)	*X albilineans* *Bacillus subtilis*	AAK15074 CAB13603	3464 bits (8983) 887 bits (2292)	0.0 0.0	1882/1882 (100%) 626/1896 (33%)	1882/1882 (100%) 938/1896 (49%)	- 140/1896 7%
PKS-3		XabB (4801 aa) PksM (4273 aa)	*X. albilineans* *B subtilis*	AAK15074 CAB13603	1274 bits (3296) 577 bits (1486)	0.0 e-163	653/653 (100%) 293/584 (50%)	653/653 (100%) 391/584 (66%)	- 17/584 (2%)
NRPS-1		XabB (4801 aa) NosA (4379 aa)	*X albilineans* *Nostoc* sp	AAK15074 AF204805	1934 bits (5010) 618 bits (1594)	0.0 e-176	1035/1046 (99%) 398/1104 (36%)	1039/1046 (99%) 586/1104 (53%)	- 86/1104 (7%)
NRPS-2		NosA (4379 aa) Peptide synthase (5060 aa)	*Nostoc sp* *Anabaena* sp	AF204805 CAC01604	416 bits (1069) 402 bits (1034)	e-115 e-111	337/1127 (29%) 315/1073 (29%)	496/1127 (43%) 479/1073 (44%)	128/1127 (11%) 114/1073 (10%)
NRPS-3		XabB (4801 aa) NosA (4379 aa)	*X albilineans* *Nostoc* sp.	AAK15074 AF204805	1847 bits (4784) 610 bits (1573)	0.0 e-173	997/1044 (95%) 392/1069 (36%)	1007/1044 (96%) 571/1069 (52%)	- 86/1069 (8%)

NRPS-4		XabB (4801 aa) NosC (3317 aa)	*X. albilineans* *Nostoc sp*	AAK15074 AAF17280	889 bits (2297) 240 bits (613)	0.0 2e-62	468/468 (100%) 156/438 (35%)	468/468 (100%) 229/438 (51%)	- 20/438 (4%)
AlbII	343	XabC (343 aa) MtmMII (326 aa) TcmO (339 aa)	*X albilineans* *Streptomyces argillaceus* *S. glaucescens*	AAK15075 AAD55584 P39896	633 bits (1633) 144 bits (361) 81.7 bits (199)	0.0 1e-34 1e-14	343/343 (100%) 98/323 (30%) 79/314 (25%)	343/343 (100%) 154/323 (47%) 140/314 (44%)	- 4/323 (1%) 12/314 (3%)
AlbIII	167	*comA* operon protein 2 (136 aa) ComAB (116 aa)	*E. coli* *Bacillus licheniformis*	AAC74756 CAA71583	133 bits (335) 97.6 bits (242)	1e-30 8e-20	68/135 (50%) 53/111 (47%)	89/135 (65%) 68/111 (60%)	- 1/111 (0%)
AlbIV	941								
PKS-4		BA3 (6359 aa) WbpG (377 aa)	*B licheniformis* *Pseudomonas aeruginosa*	AAC06348 E83253	361 bits (926) 81.6 bits (200)	2e-98 4e-15	190/441 (43%) 44/119 (36%)	267/441 (60%) 70/119 (57%)	14/441 (3%) 4/119 (3%)
AlbV	239	Thp (240 aa) IS transposase (260 aa)	*X albilineans* *Yersinia pestis*	nd AAC82714	nd 160 bits (404)	0.0 1e-38	240/240 (100%) 87/183 (47%)	240/240 (100%) 122/183 (66%)	- 2/183 (1%)

AlbVI	286	Hypothetical protein TcmP (276 aa)	*Mycobacterium tuberculosis* *Pasteurella multocida*	AAK46042 AAK03406	138 bits (347) 36.6 bits (83)	6e-32 0.24	92/224 (41%) 32/132 (28%)	125/224 (55%) 65/132 (49%)	18/224 (8%) 29/197 (6%)
AlbVII	765	4-hydroxybenzoate-CoA ligase (539 aa)	Rhodopseudomonas palustris	AAA62604	203 bits (513)	5e-51	156/492 (31%)	242/492 (48%)	31/492 (6%)
AlbVIII	330	SyrP Like (339 aa) SyrP (353 aa)	S. verticillus Pseudomonas syringae	AF210249 AAB63253	245 bits (619) 182 bits (458)	6e-64 5e-45	130/309 (42%) 106/306 (34%)	182/309 (58%) 155/306 (50%)	2/309 (0%) 4/306 (1%)
AlbIX	1959								

NRPS-6		XabB (4801 aa) DhbF (1278 aa)	*X albilineans* *B subtilis*	AAK15074 CAB15186	481 bits (1239) 354 bits (908)	e-135 1e-96	286/608 (47%) 222/608 (36%)	374/608 (61%) 341/608 (55%)	23/208 (3%) 21/608 (3%)
NRPS-7		XabB (4801 aa) NosA (4379 aa)	*X. albilineans* *Nostoc* sp.	AAK15074 AF204805	874 bits (2258) 551 bits (1420)	0.0 e-155	515/1110 (46%) 388/1148 (33%)	682/1110 (61%) 583/1148 (49%)	52/1110 (4%) 84/1148 (7%)
AlbX	83	Hypothetical protein (72 aa) MbtH (71 aa)	*P aeruginosa* *M. tuberculosis*	AAG05800 CAB08480	75.6 bits (185) 59 bits (142)	1e-13 9e-09	34/61 (55%) 25/55 (45%)	44/61 (71%) 37/55 (66%)	- -
AlbXI	315	SyrC (433 aa) Hydrolase (261 aa)	*P syringae* *S. coelicolor*	AAA85161 CAA16200	34.4 bits (78) 34 bits (77)	1.9 2.9	23/93 (24%) 19/60 (31%)	40/93 (42%) 30/60 (49%)	- -
AlbXII	451	BoxB (473 aa)	*Azoarcus evansii*	AAK00599	293 bits (751)	3e-78	174/448 (38%)	243/448 (53%)	12/448 (2%)
AlbXIII	317	Hypothetical protein (335 aa) Plasma PAF acetylhydrolase (444 aa)	*Caulobacter crescentus* *Canis familiaris*	AAK25001 AAC48484	99.5 bits (247) 37.5 bits (86)	5e-200	88/296 (29%) 43/156	125/296 (41%) 56/156	5/296 (1%) 44/156 (28%)
AlbXIV	496	Putative transmembrane efflux protein (505 aa) AlbF, putative albicidin efflux pump (496 aa)	*S coelicolor* *X albilineans*	CAB90983 AF403709	225 bits (574) 736 bits (1900)	0	154/465 (33%) 496/496 (100%)	240/465 (51%) 496/496 (100%)	8/465 (1%) -
AlbXV	584	Probable carbamoyl transferase (585 aa) BlmD (545 aa)	*P aeruginosa* *S verticillus*	AAG08390 AAG02370	201 bits (513) 192 bits (506)	1e-50 1e-47	158/458 (34%) 149/441 (33%)	222/458 (47%) 209/441 (46%)	39/458 (8%) 33/441 (7%)

AlbXVI	88	Transposase (363 aa) Transposase OrfA (88 aa)	*X. axonopodis* *Desulfovibrio vulgaris*	AF263433 AAC03166	64.8 bits (157) 61.0 bits (147)	2e-10 3e-09	27/45 (60%) 29/54 (53%)	40/45 (88%) 38/54 (69%)	- -
AlbXVII	716	Para-aminobenzoate synthase (723 aa)	*Streptomyces griseus*	CAC22117	503 bits (1295)	e-141	302/699 (43%)	409/699 (58%)	36/699 (5%)
AlbXVIII	137	4-amino-4-deoxychorismate lyase (271 aa)	*P. aeruginosa*	AAG06352	81.4 bits (200)	4e-15	46/105 (43%)	65/105 (61%)	-
AlbXIX	200	McbG (187 aa)	*E. coli*	CAA30724	60.5 bits (145)	9e-09	36/141 (25%)	58/141 (40%)	5/141 (3%)
AlbXX	202	4-hydroxybenzoate synthase (202 aa)	*E coli*	AAC77009	45.6 bits (107)	5e-04	42/161 (26%)	21/161 (13%)	-
AlbXXI	278	XabA (278aa)	*X. albilineans*	AAG28384	430 bits (1106)	0	278/278 (100%)	278/278 (100%)	-
AlbXXII	634	Heat shock protein HtpG (634) Heat shock protein HtpG (624)	*P aeruginosa* *E coli*	AAG04985 AAC73575	1051 bits (2688) 743 bits (1899)	0 0	523/634 (82%) 376/624 (60%)	588/634 (92%) 476/624 (76%)	- 4/624 (0%)

Table 5 : Comparison of conserved sequences in C domains of peptide synthestases and in putative C domains of the Alb modules

Core	Sequences conserved in peptide synthetases*	Sequence	Alb module
C1	SxAQxR(L/M)(W/Y)xL	TYAQERLWLV	NRPS-1
		STAQERMWFL	NRPS-2
		SYAQERLWLV	NRPS-3
		SLFQERLWFV	NRPS-4
		SYQQERLWFV	NRPS-7
C2	*RHExLRTxF*	RHEVLRTRF	NRPS-1 and NRPS-3
		RHAVLRTHF	NRPS-2
		RHEILRTRF	NRPS-4
		RHETLRTRI	NRPS-7
C3	*MHHxISDG(W/V)S*	IHHIISDGWS	NRPS-1 and NRPS-3
		IHHIVFDGWS	NRPS-2
		MHHLIYDAWS	NRPS-4
		MHHIICDGWS	NRPS-7
C4	YxD(F/Y)AVW	YADYALW	NRPS-1 and NRPS-3
		YADYARW	NRPS-2
		YADYAIW	NRPS-4
		YADYATW	NRPS-7
C5	(I/V)GxFVNT(Q/L)(C/A)xR	IGFFINILPLR	NRPS-1, NRPS-3 and NRPS-4
		IGLFVNTLAVR	NRPS-2
		IGFFVNILAVR	NRPS-7
C6	(H/N)QD(Y/V)PFE	HQSVPFE	NRPS-1 and NRPS-3
		HQDVPFE	NRPS-2
		NQALPFE	NRPS-4
		HRALPFE	NRPS-7
C7	RDxSRNPL	RDSSQIPL	NRPS-1 and NRPS-3
		RDTARNPL	NRPS-2
		RDTSRIPL	NRPS-4
		RDSSQIPL	NRPS-7

*Sourced from Marahiel *et al.*, 1997

Table 6 : Comparison of conserved sequences in A domains of peptide synthestases and in putative A domains of the Alb modules

Core	Sequences conserved in peptide synthetases*	Sequence	Alb module
A1	L(T/S)YxEL	WSYAQL	NRPS-1 and NRPS-3
		LSYAQL	NRPS-2
		MSYGQL	NRPS-5
		FSYRQL	PKS-4
		LSYAQL	NRPS-6 and NRPS-7
A2	LKAGxAYL(V/L)P(L/I)D	FKAGACYVPID	NRPS-1 and NRPS-3
		SLCGAASVLID	NRPS-2
		MKAGAAYVPID	NRPS-5
		LAGGLVFAPIN	PKS-4
		LKAGGCYVPLD	NRPS-6 and NRPS-7
A3	LAYxxYTSG(S/T)TGxPKG	LACVMVTSGSTGRPKG	NRPS-1 and NRPS-3
		?TRTIMVESGSLSSRLL?	NRPS-2
		PVYCIYTSGSTGSPKG	NRPS-5
		PAVMICTSGSTGTPKA	PKS-4
		LAYVMYTSGSTGRPKG	NRPS-6 et NRPS-7
A4	FDxS	FAVS	NRPS-1 and NRPS-3
		FDAA	NRPS-2
		FDLT	NRPS-5
		FAYG	PKS-4
		FAIS	NRPS-6 and NRPS-7
A5	NxYGPTE	NNYGCTE	NRPS-1 and NRPS-3
		?AAYGNAE?	NRPS-2
		NEYGPTE	NRPS-5
		DGIGCTE	PKS-4

		YIYGCTE	NRPS-6 and NRPS-7
A6	GELxIxGxG(V/L)ARGYL	GELHVHSVGMARGYW	NRPS-1 and NRPS-3
		np	NRPS-2
		GQIHIGGAGVAIGYV	NRPS-5
		GSLWVRGNTLTRGYV	PKS-4
		GEVHIESLGITHGYW	NRPS-6 and NRPS-7
A7	Y(R/K)TGDL	YKTGDM	NRPS-1 and NRPS-3
		?YKTDAL?	NRPS-2
		YASGDL	NRPS-5
		?FDTRDL?	PKS-4
		YRTGDM	NRPS-6 and NRPS-7
A8	GRxDxQVKIRGxRIELGEIE	GRQDFEVKVRGHRVDTRQVE	NRPS-1 and NRPS-3
		?GSLDVQSRIDDPRIDLCVVE?	NRPS-2
		GRKDSQIKLRGYRIELGEIE	NRPS-5
		?GRMGSAIKINGCWLSPETLE?	PKS-4
		GRRDYEVKVRGYRVDVRQVE	NRPS-6 and NRPS-7
A9	LPxYM(I/V)P	LPTYMLP	NRPS-1 and NRPS-3
		?LPDYLLP?	NRPS-2
		LPEYMLP	NRPS-5
		?LGKHHYP?	PKS-4
		LPTYMLP	NRPS-6 and NRPS-7
A10	NGK(V/L)DR	NGKLDR	NRPS-1 and NRPS-3
		?HGRVDL?	NRPS-2
		NGKVNR	NRPS-5
		?SGKVIR?	PKS-4
		NGKLDT	NRPS-6 and NRPS-7

*Sourced from Marahiel *et al.*, 1997

?: non conserved sequences

np: not present

Table 7 : Comparison of conserved sequences in PCP and TE domains of peptide synthestases and in putative PCP and TE domains of the Alb modules

Domain	Sequences conserved in peptide synthetases*	Sequence	Alb module (domain)
PCP	DxFFxxLGG(H/D)S(L/I)	D-FFAVGGHSVL	PKS-3 (PCP1)
		DNFFALGGHSLS	NRPS-1 and NRPS-3 (PCP2 and PCP4)
		DNFFELGGHSVL	NRPS-2 (PCP3)
		DNFFELGGHSLS	NRPS-5 (PCP5)
		DNFFNLGGHSLL	NRPS-6 and NRPS-7 (PCP6 and PCP7)
TE	G(H/Y)SxG	GWSSG	NRPS-7

*Sourced from Marahiel *et al.*, 1997

EXAMPLE 9: The alb carbamoyl transferase gene

albXV potentially encodes a protein of 584 aa with a predicted size of 65.2 kDa. This protein, AlbXV, is similar to BlmD, a carbamoyl transferase involved in bleomycin biosynthesis in *Streptomyces vertillus* (Du *et al.*, 2000), and to a probable carbamoyl transferase potentially expressed in *P. aeruginosa* (Table 4). High similarity of AlbXV with these proteins suggests that AlbXV is a carbamoyl transferase.

EXAMPLE 10: The alb esterase genes

albXI potentially encodes a protein of 315 aa with a predicted size of 35.9 kDa. This protein, AlbXI, exhibits low similarity to SyrC, a putative thioesterase involved in syringomycin biosynthesis by *Pseudomonas syringae* (Zhang *et al.*, 1995), and to a potential hydrolase encoded by *Streptomyces coelicolor* (Table 4). Precise function of SyrC remains unknown but SyrC is similar to a number of thioesterases, including fatty acid thioesterases,

haloperoxidases, and acyltransferases that contain a characteristic GxCxG motif. The corresponding SyrC domain GICAG is conserved in AlbXI which contains the sequence GWCQA, except that A replaces the last G, suggesting that AlbXI may be an esterase despite its low overall similarity with SyrC.

albXIII potentially encodes a protein of 317 aa with a predicted size of 34.5 kDa. This protein, AlbXIII, is similar to hypothetical proteins with unknown function from several bacteria including *Caulobacter crescentus* (Table 4). AlbXIII and these hypothetical proteins contain a GxSxG motif characteristic of serine esterases and thioesterases, the corresponding sequence in AlbXIII being GHSVG. In addition, AlbXIII presents a similarity with the 2-acetyl-1alkylglycerophosphocholine esterase which hydrolyzes the platelet-activating factor in *Canis familiaris* (Table 4), suggesting that AlbXIII is an esterase.

EXAMPLE 11: The alb methyltransferase genes

albII potentially encodes a protein of 343 aa (AlbII) with a predicted size of 37.7 kDa. *albII* is 100% identical to the *xabC* cistron, previously described as encoding an *O*-methyltransferase downstream *xabB* (Huang *et al.*, 2000a). This conclusion is based on the similarity of XabC with a family of methyltransferases that utilize S-adenosyl-L-methionine (SAM) as a co-substrate for *O*-methylation including TcmO protein from *Streptomyces glaucescens* (Huang *et al.*, 2000a). AlbII contains three highly conserved motifs of SAM-dependent methyltransferases, including the motif I involved in SAM binding (Figure 3). In the Figure, identical or similar amino acids (A=G ; D=E ; I=L=V) are shown in bold. Numbers indicate the position of the amino acid from the N-terminus of the protein. Abbreviations used in the Figure are: Sgl-TcmO and Sgl-TcmN, multifunctional cyclase-hydratase-3-*O*-Mtase and tetracenomycin polyketide synthesis 8-*O*-Mtase of *Streptomyces glaucescens*, respectively (accession number: M80674); Smy-MdmC, midecamycin-*O*-Mtase of *Streptomyces mycarofaciens* (accession number: M93958); Mxa-SafC, Saframycin *O*-Mtase of *Myxococcus xanthus* (accession number: U24657); Ser-EryG, erythromycin biosynthesis *O*-Mtase of *Saccharopolyspora erythraea* (accession number: S18533); Spe-DauK, carminomycin 4-O-Mtase of *Streptomyces peucetius* (accession number: L13453); Sal-DmpM, *O*-demethylpuromycin-*O*-Mtase of *Streptomyces alboniger* (accession number: M74560); Shy-RapM, rapamycin *O*-Mtase of *Streptomyces hygroscopicus* (accession number: X86780); Sav-AveD, avermectin B 5-*O*-Mtase of *Streptomyces avermitilis* (accession number: G5921167), Sar-Cmet, mithramycin *C*-methyltransferase of *Streptomyces argillaceus* (accession number: AF077869); AlbII, putative albicidin biosynthesis *C*-

Methyltransferase of *Xanthomonas albilineans* (SEQ ID No. 27) ; identical to XabC, accession number: AF239749).

Comparison of AlbII with the Genbank database revealed that AlbII, besides 100% identity to XabC, exhibited the highest degree of overall identity with MtmMII, a *C*-methyltransferase from *Streptomyces argillaceus* (Table 4) involved in *C*-methylation of the polyketide chain for mithramycin biosynthesis, suggesting that AlbII is a *C*-methyltransferase. XabC was not compared by Birch and co-workers with MtmMII (Huang *et al.*, 2000a) because the MtmMII sequence was not available until recently in the Genbank database. The three highly conserved motifs in SAM methyltransfererases are also present in MtmMII (Figure 3), suggesting that AlbII is a *C*-methyltransferase SAM-dependent.

albVI potentially encodes a protein of 286 aa (AlbVI) with a predicted size of 32.1 kDa similar to several hypothetical protein from *Mycobacterium tuberculosis* (Genbank accessions n° AAK46042, AAK48238, AAK44517, AAK46218) and from *S. coelicolor* (Genbank accession n° CAC03631). AlbVI is also similar to the tetracenomycine C synthesis protein (TcmP) of *Pasteurella multocida* (Table 4). Four highly conserved motifs in TcmP and other *O*-methyltransferases are also present in AlbVI (Figure 4), suggesting that AlbVI is an *O*-methyltransferase. In the Figure, identical or similar aa (A=G ; D=E ; I=L=V ; K=R) are shown in bold. Numbers indicate the position of aa from the N-terminus of the protein. Abbreviations used in the Figure are: Sgl-tcmP, tetracenomycin C synthesis protein of *Streptomyces glaucescens* (accession number: C47127); Sme-PKS, putative polyketide synthase of *Sinorhizobium meliloti* (accession number: AAK65734); Pmu-tcmP: tetracenomycin C synthesis protein of *Pasteurella multocida* (accession number: AAK03406); Mtu-Omt: putative *O*-methyltransferase of *Mycobacterium tuberculosis* (accession number: AAK45444); Mlo-Hp: hypothetical protein containing similarity to *O*-methyltransferase of *Mesorhizobium loti* (accession number: BAB50127); Mtu-Hp1: hypothetical protein of *Mycobacterium tuberculosis* (accession number: AAK46042); Mtu-Hp2: hypothetical protein of *Mycobacterium tuberculosis* (accession number: AAK48238); Mtu-Hp3: hypothetical protein of *Mycobacterium tuberculosis* (accession number: AAK44517); AAK46218); Sco-Hp: hypothetical protein of *Streptomyces coelicolor* (accession number: CAC03631); AlbVI, putative albicidin biosynthesis *O*-Methyltransferase of *Xanthomonas albilineans* (this study). The three highly conserved motifs in SAM methyltransfererases are not present in AlbVI, indicating that SAM is not a co-substrate of AlbVI.

EXAMPLE 12: The alb derived-benzoate products biosynthesis genes

alb*XVII* potentially encodes a protein of 716 aa with a predicted size of 79.8 kDa. This protein, AlbXVII, is very similar to the para-aminobenzoate (PABA) synthase from *Streptomyces griseus* (Table 4). This enzyme is required for the production of the antibiotic candicidin (Criado *et al.*, 1993).

albXVIII potentially encodes a protein of 137 aa with a predicted size of 15.0 kDa. This protein, AlbXVIII, is similar to the 4-amino-4-deoxychorismate lyase (ADCL) from *P. aeruginosa* (Table 4). The function of ADCL is to convert 4-amino-4-deoxychorismate into PABA and pyruvate. The length of AlbXVIII is smaller (Table 4) than the length of ADCL and the similarity of AlbXVIII with this protein starts only at residues 161. *albXVIII* is preceded by a small ORF encoding a sequence of 59 aa similar to the first 42 amino acids of ADCL from *P. aeruginosa*. These data suggest that *albXVIII* is probably a truncated form of *albXVIII* and probably not functional. *albXVIII* may, therefore, not be involved in albicidin biosynthesis. The region between *albXVII* and *albXVIII* was amplified by PCR from total DNA of *X. albilineans* Xa23R1 strain using primers ORFW (5'gcgagaggacaagctgctgc3') SEQ ID No. 53 and ORFY (5'cgttgaggatgcagcgctcg3') SEQ ID No. 54 and was sequenced. Resulting sequence data showed that the sequence of the PCR fragment was 100% identical to the sequence of pALB540, indicating that the recombination of *albXVIII* did not occur during cloning of the genomic fragment in pALB540.

albXX potentially encodes a protein of 202 aa with a predicted size of 22.6 kDa. This protein AlbXX is similar to the 4-hydroxybenzoate synthase potentially involved in ubiquinone biosynthesis by *Escherichia coli* (Siebert *et al.*, 1992).

EXAMPLE 13: The alb regulatory genes

albIII potentially encodes a protein of 167 amino acids with a predicted size of 17.8 kDa that is similar to the transcription factors ComA of different bacteria such as *E. coli* and *B. licheniformis* (Table 4). ComA transcription factors appear to be involved in regulation of antibiotic production in bacteria. In *E. coli*, a gene similar to *comA* is present in the enterobactin biosynthesis gene cluster (Liu *et al.*, 1989). In *B. subtilis*, ComAB was described as a probable positive activator of lichenysin synthetase transcription (Yakimov *et al.*, 1998) and a gene similar to *comA* was shown to be essential for bacilysin biosynthesis (Yazgan *et al.*, 2001). These data suggest that AlbIII regulates transcription of genes involved in albicidin biosynthesis.

albVIII potentially encodes a protein of 330 aa with a predicted size of 37.7 kDa. This

protein, AlbVIII, is very similar to the SyrP like protein from *S. verticillus* and to SyrP protein from *P. syringae* (Table 4). SyrP participates in a phosphorylation cascade controlling syringomycin synthesis (Zhang *et al.*, 1997) and the *syrP* like gene was described in the *S verticillus* bleomycin biosynthetic gene cluster (Du *et al.*, 2000). These data suggest that AlbVIII regulates albicidin biosynthesis in *X. albilineans*.

EXAMPLE 14: The alb resistance genes

albXIV potentially encodes a protein of 496 aa with a predicted size of 52.7 kDa. This protein, AlbXIV, is 100% identical to AlbF isolated from *X. albilineans* strain Xa13 (GenBank Accession AF403709; direct submission by Bostock and Birch and described as "a putative albicidin efflux pump which confers resistance to albicidin in *E. coli*"). AlbXIV and AlbF are closely related to a family of transmembane transporters involved in antibiotic export and antibiotic resistance in many antibiotic-producing organisms. AlbXIV and AlbF exhibited the highest degree of overall identity with the putative transmembrane efflux protein from *S. coelicolor* (Table 4). These data suggest that AlbXIV and AlbF may be involved in albicidin resistance by transporting the toxin out of the bacterial cells that produce it. Alternatively, AlbXIV and AlbF may simply play a role in antibiotic secretion and/or plant pathogenesis to effect the transport of albicidin outside of producing cells.

albXIX potentially encodes a protein of 200 aa with a predicted size of 22.8 kDa. This protein, AlbXIX, is similar to the McbG protein from *E. coli* (Table 4). In *Enterobacteriae*, the McbG protein, together with two other proteins (McbE and McbF), was shown to cause immunity to the peptide antibiotic microcin B17 which inhibits DNA replication by induction of the SOS repair system (Garrido *et al.*, 1988). McbE and McbF proteins serve as a pump for the export of the active antibiotic from the cytoplasm, whereas a McbG alone also provides some protection: a well-characterized deficient-immunity phenotype is exhibited by microcin B17-producing cells in the absence of the immunity gene mcbG (Garrido *et al.*, 1988). The significant similarity between AlbXIX and McbG, together with the fact that albicidin also blocks DNA replication (Birch and Patil, 1985a) suggests that AlbXIX confers immunity against albicidin in *X. albilineans*.

EXAMPLE 15: Transposition proteins

albV is 100% identical to the *thp* gene described in a divergent position upstream from *xabB* (Huang *et al.*, 2000a). The *thp* gene potentially encodes a protein of 239 aa displaying significant similarity to the IS21-like transposition helper proteins. In *X. albilineans* strain

LS155 from Australia, insertional mutagenesis of *thp* blocked albicidin production, but *trans*-complementation failed, indicating the involvement in albicidin production of a downstream gene in the *thp* operon (Huang *et al.*, 2000a).

albXVI potentially encodes a protein of 88 aa with a predicted size of 9.8 kDa similar to the transposases from several bacteria such as *Xanthomonas axonopodis* or *Desulfovibrio vulgaris* (Table 4).

The presence of transposition proteins in the XALB1 cluster is probably a remnant from a past transposition event that may have contributed to the development of the albicidin XALB1 cluster.

EXAMPLE 16: Unknown functions

AlbX potentially encodes a protein of 83 aa with a predicted size of 9.4 kDa. This protein, AlbX, is similar to an hypothetical protein from *P. aeruginosa* and to the MbtH protein from *Mycobacterium tuberculosis*. MbtH is a protein with unknown function found in the mycobactin gene cluster (Quadri *et al.*, 1998). A MbtH-like protein with unknown function was also described in the bleomycin biosynthetic gene cluster of *S. verticillus* (Du *et al.*, 2000). These data suggest that AlbX is involved in albicidin biosynthesis but its function remains unknown.

albXII potentially encodes a protein of 451 aa with a predicted size of 51.6 kDa. This protein, AlbXII, is very similar to a protein of 55 kDa encoded by the *boxB* gene in *Azoarcus evansii* (Table 4). This protein is a component of a multicomponent enzyme system involved in the hydroxylation of benzoyl CoA, a step of aerobic benzoate metabolism in *Azoarcus evansii*, but its function remains unknown (Mohamed *et al.*, 2001).

EXAMPLE 17: Prediction of amino acid specificity of Alb NRPS modules

In NRPSs, specificity is mainly controlled by A domains which select and load a particular amino-, hydroxy- or carboxy-acid unit (Marahiel *et al.*, 1997). The substrate-binding pocket of the phenylalanine adenylation (A) domain of the gramicidin S synthetase (GrsA) from *Brevibacillus brevis* was recently identified by crystal structure analysis as a stretch of about 100 amino acid residues between highly conserved motifs A4 and A5 (Conti *et al.*, 1997). Based on sequence analysis of known A domains, in relation to the crystal structure of the GrsA (Phe)substrate binding pocket, similar models have been published to predict the amino acid substrate which is recognized by an unknown NRPS A domain (Challis *et al.*, 2000; Stachelhaus *et al.*, 1999). These models postulate specificity-conferring codes for

A domains of NRPS consisting of critical amino acid residues putatively involved in substrate specificity. The model proposed by Marahiel and co-workers (Stachelhaus *et al.*, 1999) defined a signature sequence consisting of ten amino acids lining with the ten residues of the phenylalanine-specific binding pocket located at positions 235, 236, 239, 278, 299, 301, 322, 330, 331 and 517 in the GsrA (Phe) sequence (accession number: P14687). The model proposed by Townsend and co-workers (Challis *et al.*, 2000) uses only the first eight of these critical residues.

Preliminary specificity assignments of albicidin synthase AlbI, AlbIV, AlbVII and AlbIX NRPS modules were made by comparison of complete sequences between conserved motifs A4 and A5 with sequences in the Genbank database. The corresponding sequence of the AlbIV NRPS-5 module is most related to domain 5 of bacitracin synthase 3 (BA3) from *B. licheniformis* that was suggested to activate Asn (Konz *et al.*, 1997). Corresponding sequences of AlbI and AlbIX NRPS-1, NRPS-3, NRPS-6 and NRPS-7 modules, apart from their very high similarity with XabB, exhibited the highest degree of overall identity (39%) with the Blm NRPS2 module of the biosynthetic gene cluster for bleomycin from *S. verticillus* that specifies for β-Alanine (Du *et al.*, 2000). The corresponding sequence of AlbVII PKS-4 produced the highest significant alignment with acetate-CoA ligase from *Sulfolobus solfataricus* (Genbank accession number: AAK41550), aryl-CoA ligase from *Comamonas testosteroni* (Genbank accession number: AAC38458) and 4-hydroxybenzoate-CoA ligase from *R. palustris*. The sequence between motifs A4 and A5 of the AlbI NRPS-2 could not be significantly aligned with any sequence present in the Genbank database. Comparison of this sequence with the corresponding sequence of GrsA (Phe) revealed that parts of the putative core and structural "anchor" sequences of AlbI NRPS-2 are deleted (Figure 5), suggesting that the AlbI NRPS-2 substrate binding pocket is not functional. In the Figure, amino acids of the six Alb NRPSs and of Alb PKS-4 that are identical or similar to GrsA or Blm sequences (A=G; D=E; I=L=V; R=K) are shown in bold. Amino acids underlined in the GsrA sequence correspond to the phenylalanine-specific binding pocket. The positions of these amino acids in the GrsA primary sequence are indicated at the top of the figure. Amino acids underlined in the other sequences correspond to putative constituents of binding pockets, aligned with the seven residues of the phenylalanine- specific binding pocket of GrsA. Shaded amino-acids correspond to the putative core sequences and structural 'anchors' based on comparison with the GrsA binding-pocket structure.

Alignment of the primary sequence between conserved motifs A4 and A5 of the AlbI, AlbIV, AlbVII and AlbIX NRPS-1, NRPS-3, NRPS-5, NRPS-6, NRPS-7 and PKS-4 modules

with the corresponding sequence of GrsA (Phe) (Figure 5) revealed the putative constituents of binding pockets that constitute the codes as defined by Marahiel and co-workers (Stachelhaus *et al.*, 1999). These codes were compared with those of proteins most related to the sequence between the A4 and A5 motifs (Table 8) and were analyzed with the model proposed by Townsend and co-workers (Challis *et al.*, 2000, http://jhunix.hcf.jhu.edu/~ravel/nrps//). Using these codes, we were able to predict the Asparagine specificity of the AlbIV NRPS-5 module. The AlbIV NRPS-5 signature is 100% identical to BacC-M5 (Asn) and TyrC-M1 (Asn) codes identified in bacitracin synthetase 3 from *B. licheniformis* and in tyrocidine synthetase 3 from *B. brevis* (Table 8). The AlbIV NRPS-5 signature is also identical to the Asn code defined by Marahiel and co-workers (1997), except that I is replaced by L at position 299 (Table 8). The AlbI and AlbIX NRPS-1, 3, 6 and 7 signatures did not match any of those defined by Marahiel and co-workers (1997). Similarly, convincing predictions using the model proposed by Townsend and co-workers were not obtained either (Challis *et al.*, 2000, http://jhunix.hcf.jhu.edu/~ravel/nrps//). The AlbI and AlbIX NRPS-1, 3, 6 and 7 signatures diverged from all NRPS signatures previously described, except from the XabB signature that is identical to the AlbI NRPS-1 and 3 signatures. The signature most closely related to AlbI NRPS-1 and 3 specify Pro and the signature most closely related to AlbIX NRPS-6 and 7 specify Ser, but the degree of similarity in both cases is very weak (Table 8). The PKS-4 signature is similar to the AlbI NRPS-1 and NRPS-3 signatures at positions 235, 299 and 301.

Analysis of alignment of the primary sequence between conserved motifs A4 and A5 of the AlbI and AlbIX NRPS-1, NRPS-3, NRPS-6 and NRPS-7 modules with the corresponding sequences of the bleomycin synthase (Blm) NRPS2 (β-Ala) and gramicidin S synthetase (GrsA) modules (Figure 5) revealed that (i) sequences of AlbI NRPS-1 and AlbI NRPS-3 differ only at the level of two residues that are not involved in substrate binding, (ii) sequences of AlbIX NRPS-6 and AlbIX NRPS-7 are 100% identical, (iii) sequences of AlbI NRPS-1 and AlbI NRPS-3 are very similar to sequences of AlbIX NRPS-6 and AlbIX NRPS-7 but differ at the level of five putative constituents of binding pocket, (iv) AlbI and AlbIX NRPS residues, which are similar to residues of Blm NRPS2 (β-Ala) or GrsA (Phe), are essentially located at the level of the putative core sequences and structural "anchor", and differ at the level of putative constituents of the binding pocket.

Binding-pocket constituents forming the NRPS signatures have been classified into three subgroups according to their variability among 160 specificity–conferring signature sequences (Stachelhaus *et al.*, 1999): (i) invariant residues Asp235 and Lys517 that mediate

key interactions with the α-amino and α-carboxylate group of the substrate, respectively; (ii) moderately variant residues in positions 236, 301 and 330 which correspond to aliphatic amino acids and which may modulate the catalytic activity and fine-tune the specificity of the corresponding domains; (iii) highly variant residues in positions 239, 278, 299, 322 and 331 which may facilitate substrate specificity. AlbI and AlbIX NRPS-1, 3, 6 and 7 signatures are not totally in accordance with this classification. Invariant residue Lys517 is conserved in the four NRPS signatures, indicating the presence of an α-carboxylate group in the corresponding substrates. The Asp235Ala alteration is not consistent with an α-amino acid substrate. Birch and co-workers (Huang *et al.*, 2001) assumed that the initial alanine residue in the XabB signature was consistent with a nonproteinogenic hydroxy acid substrate by analogy with the initial glycine in the signature of the hydroxyisovaleric-acid (HVCL) loading domain of enniatin synthetase. The presence of an initial Alanine in the AlbVII PKS-4 signature (Figure 8) and in several 4-hydroxybenzoate–CoA ligase codes may confirm this hypothesis. However, the HVCL loading domain of enniatin synthetase (Table 8) and AlbVII PKS-4 are not preceded by a C domain and are not followed by a PCP domain, in contrast to the AlbI and AlbIX NRPS-1, 3, 6 and 7 modules. An Asp235Val alteration was recently described in the β-Ala specificity-conferring code (Du *et al.*, 2000, Table 8), suggesting that the substrate of AlbI and AlbIX NRPS-1, 3, 6 and 7 modules may be different from α-amino acids but may contain an amino group. Residue 236 is an aliphatic residue (Val or Ile) in all AlbI and AlbIX NRPS-1, 3, 6 and 7 signatures. Residue 301 is an aliphatic residue (Ala) in the AlbI NRPS-1 and 3 codes, but it is a Ser in the AlbIX NRPS-6 and 7 signatures. Residue 330 is not an aliphatic residue in the four NRPS signatures but an Asp. Similar alterations are present in the β-Ala code: residue 236 is an Asp, residue 301 is a Ser and residue 330 is an aliphatic amino acid. Concerning highly variable residues, AlbI NRPS-1 and 3 signatures differ from AlbIX NRPS-6 and 7 signatures at residue positions 299, 322 and 331, confirming that both types of NRPS modules specify different substrates.

Table 8 : Comparison of signature sequences, as defined by Marahiel and co-workers (Stachelhaus *et al.*, 1999), derived from sequences between the A4 and A5 domains of the AlbI, AlbIV, and AlbIX NRPS modules with those of Tyr-M1 (Pro) (Tyrocidine synthetase 2 module 1, accession number: AAC45929), VirS (Pro) (Virginiamycin S synthetase, accession number : CAA72310), HVCL (hydroxyisovaleric acid-CoA ligase, ACL1 enniatin synthetase, accession number: S39842), EntF-M1 (Ser) (Enterobactin synthase, accession number: AAA92015), β-Ala code (β-Ala selectivity-conferring code defined by Du *et al.* , 2000),

BacC-M5 (Asn) (Bacitracin synthetase 3, accession number: AAC06348), TyrC-M1 (Asn) (Tyrocidine synthetase 3, accession number: AAC45930) and Asn code (Asn selectivity-conferring code defined by Marahiel and co-workers (Stachelhaus *et al.*, 1999). Amino acids of AlbI NRPS-1 and NRPS-3 signatures identical or similar to TyrB-M1 (Pro), VirS (Pro) and HVCL signatures (A=G; D=E; I=L=V; R=K) are shown in bold. Amino acids of AlbIX NRPS-6 and NRPS-7 signatures identical or similar to Vir (Pro) and Blm (β-Ala) signatures (A=G; D=E; I=L=V; R=K) are shown in bold. Variability: 0 indicates invariant residues, +/- moderately variant residues and ++ highly variant residues.

	Position in GsrA (Phe) and variability									
Domains	235	236	239	278	299	301	322	330	331	517
	0	+/-	++	++	++	+/-	++	+/-	++	0
Alb NRPS-1	**A**	**V**	K	**Y**	**V**	**A**	**N**	D	A	K
Alb NRPS-3	**A**	**V**	K	**Y**	**V**	**A**	**N**	D	A	K
TyrB-M1 (Pro)	D	**V**	Q	S	**I**	**A**	**N**	**V**	**V**	K
VirS (Pro)	D	**V**	Q	**Y**	**A**	**A**	**H**	**V**	**M**	K
HVCL	**G**	**A**	**L**	**H**	**V**	**V**	**G**	**S**	**I**	K
Alb NRPS-6	**A**	**I**	K	**Y**	**F**	**S**	**I**	D	**M**	K
Alb NRPS-7	**A**	**I**	K	**Y**	**F**	**S**	**I**	D	**M**	K
VirS (Pro)	D	**V**	Q	**Y**	**A**	**A**	**H**	**V**	**M**	K
EntF-M1 (Ser)	D	**V**	W	**H**	**F**	**S**	**L**	**V**	D	K
β-Ala code	**V**	D	**W**	**V**	**I**	**S**	**L**	A	D	K
Alb NRPS-5	D	L	T	K	I	G	E	V	G	K
BacC-M5 (Asn)	D	L	T	K	I	G	E	V	G	K
TyrC-M1 (Asn)	D	L	T	K	I	G	E	V	G	K
Asn code	D	L	T	K	L	G	E	V	G	K

EXAMPLE 18: Identification of putative promoters and putative terminators in XALB1

Putative rho independent terminators were identified downstream from *albIV* and *albXVI* using the Terminator program (Brendel and Trifonov, 1984), run with the Wisconsin Package™ GCG software (Figure 6). In the Figure, dashes indicate palindromic sequences. Symbols used in the Figure are: P, Primary structure value of putative terminator (minimum threshold value of 3.5 represents 95 percent of known, factor-independent, prokaryotic terminators); S, Secondary structure value of putative terminator. The presence of these

terminators confirmed the proposed genetic organization of operons 1 and 3. A rho-independent terminator was identified in the intergenic region between *albXVII* and *albXVIII*, suggesting that the group of genes initially supposed to be organized in operon 4 may be in fact organized in two operons, operon 4 formed by *albXVII* and operon 5 by *albXVIII – albXX*. No putative rho independent terminator was found downstream from *albIX* and from *albXX*.

The 236 bp region between *albI* (operon 1) and *albV* (operon 2) is 100% identical to the sequence between *xabB* and *thp* genes that is assumed to contain a bidirectional promoter (Huang *et al.*, 2000a and 2001), suggesting that transcription of operon 1 and 2 is regulated by the same bidirectional promoter region (Huang *et al.*, 2001).

The 412 bp region comprised between *albX* (operon 3) and *albXVII* (operon 4) also contains a putative bidirectional promoter (Figure 7). In the Figure, the sequence of putative promoters are underlined, and putative ATG or TTG start codons are in bold. The closest matches (TTGACA-18x-TATAGT) to the consensus -35 (TTGACA) and -10 (TATAAT) sequences for *E. coli* σ^{70} promoters occurs 61 bp upstream from *albX* (operon 3). The closest matches (TTCAGA-19x-TATACA) to the consensus sequences for *E. coli* σ^{70} promoters occur 320 bp upstream from *albXVII* (operon 4). The region between *albXVII* and *albXVIII* lacks any apparent *E. coli* σ^{70} promoter. However, the sequence immediately upstream from *albXIX*, corresponding to the coding sequence of *albXVIII*, potentially contains an unidirectional promoter (Figure 7) . The closest match (TTGCTC-19x-TATATT) to the consensus sequences for *E. coli* σ^{70} promoters occurs 33bp upstream from *albXIX*. The presence of a terminator downstream from *albXVII* and of a promoter upstream from *albXIX* suggests that *albXVIII* is not transcribed and that *albXIX* and *albXX* form operon 5.

EXAMPLE 19: Cloning of the XALB2 gene cluster

The 6 kb *Eco*R I fragment carrying Tn*5* and flanking sequence from strain AM37 was cloned in pBR325 and the obtained plasmid was designated pAM37 (Table 1). A 1.1 kb *Hin*d III-*Hin*d III DNA fragment from pAM37, named PR37 (Table 1), was labeled with ^{32}P and used to probe the 845 clones from the genomic library of *X. albilineans* strain Xa23R1, previously described (Rott et al., 1996). Eight new cosmids hybridized to this probe and restored albicidin production in mutant AM37. One of these cosmid, pALB389, carrying an insert of about 37 kb (Table 1), was used for complementation studies of the five mutants not complemented by pALB540 and pALB571. Cosmid pALB389 complemented mutants AM10

and AM37. Mutant AM10 was initially thought to be complemented by pALB639 (Rott et al., 1996). However, further complementation studies showed that mutant AM10 was not complemented by pALB639 and that only three mutants (AM12, AM13 and AM36) were complemented by pALB639 containing the third genomic region XALB3 involved in albicidin production. A 3 kb *Eco*RI- *Eco*RI DNA fragment from pALB389 that hybridized with probe PR37 was sub-cloned in pUFR043 (Table 1). The resulting plasmid pAC389.1 complemented mutants AM10 and AM37, confirming that the second region involved in albicidin production, XALB2, was present in the 3 kb insert of pAC389.1.

EXAMPLE 20: Cloning of the XALB3 gene cluster

Cosmid pALB639, carrying an insert of 36 kb (Rott *et al.*, 1996; Table 1) was used as a probe to compare the *Eco*RI restriction profiles of *X. albilineans* strain Xa23R1 with those of mutants AM12, AM13 and AM36 which were supposed to be mutated in the XALB3 gene cluster. An 11 kb band which was found in strain Xa23R1 but not in the three mutants was supposed to contain the XALB3 gene cluster. A 9.7 kb *Eco*RI DNA fragment purified from cosmid pALB639 also used as a probe in Southern blot analyse revealed the same 11 kb band. This 9.7 kb *Eco*RI DNA fragment was sub-cloned in pUFR043 (Table 1) and the resulting plasmid pAlb639A complemented mutants AM12, AM13 and AM36. The third region involved in albicidin production, XALB3, was therefore present in the 9.7 kb insert of pAlb639A.

EXAMPLE 21: Sequencing of the Tn*5* insertional site of tox$^-$ mutants located in XALB2 and XALB3 and sequencing of the genomic regions XALB2 and XALB3

In Figure 8, E, H, Sa and S indicate restriction endonuclease cut sites for *Eco*RI, *Hin*dIII, *Sal*I and *Sau*3AI, respectively. The DNA inserts carried by plasmids pAC389.1, pALB639A or pEV639 are represented by the bars at the top of the respective figures. Positions of the Tn*5* insertional sites of mutants AM10, AM12, AM36 and AM37 were determined by sequencing and are indicated by vertical arrows. The DNA region corresponding to the Tn*5* flanking regions in pAM10, pAM12.1, pAM36.2 and pAM37 and in the PR37 DNA fragment are represented by the bars at the bottom of the respective figures. The location and direction of *albXXI* and *albXXII* are indicated by thick black arrows. The location of other orfs in XALB2 similar to those described by Huang et al. (2000b) are indicated by thick white arrows.

The 7 kb *Eco*R I fragment carrying Tn*5* and flanking sequence from strain AM10 was cloned in pBluescript II KS (+), and the obtained plasmid was designated pAM10 (Table 1). The sequences between *Eco*RI sites and the Tn*5* insertional site of mutants AM10 and AM37 were sequenced from the resulting plasmids pAM10 and pAM37, respectively. The complete double-strand nucleotide sequence of the 2,986 bp *Eco*R I – *Eco*R I insert of pAC389.1 was determined from sequencing results of plasmids pAC389.1, pAM10 and pAM37 (Figure 8). The Tn*5* *in*sertional sites of mutants AM10 and AM37 were sequenced from plasmids pAM10 and pAM37 (Table 1), respectively, using the sequencing primer GUSN (5'tgcccacaggccgtcgagt3') that annealed 135 bp downstream from the insertional sequence IS50L of Tn*5*-*gusA*. The Tn*5* insertional site of AM10 and AM37 was located at position 2107 and 1882, respectively.

The *Eco*RI fragments carrying Tn*5* and the flanking sequences from mutants AM12 and AM36 were cloned in pBR325 (Rott *et al.*, 1996; Table1). The sequences between *Eco*RI site and the Tn*5* insertional site of mutants AM12 and AM36 were sequenced from the resulting plasmids pAM12.1 and pAM36.2, respectively. The complete double-strand nucleotide sequence of the 9,673 bp *Eco*R I – *Sau*3A I insert of pALB639A was determined from the sequencing results of plasmids pAM12.1, pAM36.2 and pALB639A (Figure 8). The Tn*5* insertional site of mutants AM12 and AM36 was sequenced from plasmids pAM12.1, pAM36.2 using the sequencing primer GUSN (5'tgcccacaggccgtcgagt3') that annealed 135 bp downstream from the insertional sequence IS50L of Tn*5*-*gus*A. The Tn*5* insertional site of AM12 and AM36 was located at position 6500 and 7232, respectively (Figure 8).

EXAMPLE 22: Homology analysis and genetic organization of XALB2 (Figure 8).

The sequence of 2986 bp containing XALB2 is 99.4% identical to the sequence of 2989 bp containing *xabA* described in *X. albilineans* strain LS155 from Australia (Huang et al., 2000b; accession number AF191324). The Tn*5* insertional site of mutant LS156 described in *xabA* is 15 bp upstream from the insertional site of AM37. The orf disrupted in AM37 and AM10, designed albXXI, is identical to *xabA* except a C which replaces a T at position 1642. albXXI potentially encodes a protein of 278 aa with a predicted size of 29.3 kDa which is 100% identical to the potential product of xabA, described as a phosphopantetheinyl transferase (Huang et al., 2000b). Region XALB2 contains three additional orfs (orf1, orf2, and orf3) similar to those described by Huang et al., (2000b; orf, rsp6 and aspT). orf2 and orf3 are 100% identical to rsp6 and aspT respectively, and orf1 is similar to but smaller than orf. There are no close matches to the *E. coli* γ70 promoter –10 (TATAAT) and –35 (TTGACA)

consensus sequence, and no putative RBS site upstream from the putative start codon ATG of albXXI. The putative factor-independent transcription site described at 42 bp downstream from the TGA stop codon of xabA (Huang et al., 2000b) is also present at the same position downstream from albXXI.

EXAMPLE 23: Homology analysis and genetic organization of XALB3 (Figure 8).

The orf disrupted in mutants AM12 and AM36 was located between nucleotide 6090 (ATG) and 8009 (TAA) and was designed *albXXII*. The first ATG at position 6090 is not preceded by a putative ribosome binding sequence, suggesting that the start codon is the ATG at position 6105 which is preceded at position –9 by the putative ribosome binding site sequence GGAG. A putative rho independent terminator was identified at position 8082, 73 b downstream from *albXXII* (figure 6). There are no close matches to *E. coli* σ^{70} promoter –10 (TATAAT) and –35 (TTGACA) consensus sequence upstream from the putative start codon. The *Sal*I DNA fragment corresponding to DNA sequence from nucleotide 5510 to nucleotide 8124, which contains the 595 bp upstream from the putative start codon, the orf *albXXII* and the putative rho independent terminator, was sub-cloned in pUFR043 in the opposite direction to LacZ (Table 1). The resulting plasmid pEV639 (table 1) complemented mutants AM12, AM13 and AM36, confirming that (i) the third region involved in albicidin production, XALB3, was present in the insert of pEV639; (ii) *albXXII* is not transcribed as part of a larger operon ; and (iii) the 595 bp upstream the putative start codon contain a promoter.

The potential product of *albXXII*, designated AlbXXII, is a protein of 634 aa with a predicted size of 71.5 kDa. This protein is very similar to the heat shock protein HtpG from *Pseudomonas aeruginosa* (identities = 82%) and from *Escherichia coli* (identities = 60%)(table 4). The methionine encoded by the putative start codon at position 6105 was aligned with the first aminoacid of the heat shock protein HtpG from *Pseudomonas aeruginosa*, confirming that *albXXII* initiates at position 6105.

The invention includes the isolation and sequencing of a region of 55,839 bp from *X. albilineans* strain Xa23R1 containing the major gene cluster XALB1 involved in albicidin production. Analysis of this region allowed us to predict the genetic organization of the gene cluster XALB1 which contains 20 ORFs grouped in four or five operons (Figure 1). Because *albXVIII* is a truncated gene, XALB1 genes may be organized in five operons. Therefore, we will from now on consider *albXVII* as part of operon 4 and *albXIX* and *albXX* as part of operon 5. Similar operon-type organizations for antibiotic biosynthesis clusters are well

known and have been postulated to facilitate cotranslation of genes within the operon to yield equimolar amounts of proteins for optimal interactions to form the biosynthesis complexes (Cane, 1997). Overlapping genes involved in the same process are also quite common in bacteria (Normark *et al.*, 1983).

Previous results of transposon mutagenesis and complementation studies (Rott *et al.*, 1996; Rott, unpublished results) are in accordance with the predicted genetic organization of XALB1 described in this study, and allowed us to establish that operons 1, 2 and 3 are involved in albicidin biosynthesis: (I) Tox$^-$ mutants with a Tn*5-gusA* insertion site located in DNA fragments B, C, G and D were complemented by cosmid pALB571 and not by cosmid pALB540, confirming that cosmid pALB571 potentially contains the entire operon 1; (ii) Tox$^-$ mutants with a Tn*5-gusA* insertion site located in DNA fragments A and H were complemented by both cosmids pALB540 and pALB571, confirming that both cosmids potentially contain the entire operon 2; (iii) mutant XaAM1 with a Tn*5-gusA* insertion site located in DNA fragment J is the only Tn*5* Tox$^-$ mutant complemented by cosmid pALB540 and not by cosmid pALB571, confirming that cosmid pALB540 potentially contains the entire operon 3. Our mutagenesis studies did not confirm that operons 4 and 5 are required for biosynthesis of albicidin. The para-aminobenzoate (PABA) is required for the growth of many bacteria probably including *X. albilineans*, suggesting that a mutation in *albXVII* may be lethal and explaining why we did not obtain any mutant disrupted in this gene.

Putative bidirectional promoters were identified between operons 1 and 2 (Huang et al., 2001) and between 3 and 4 (Figure 7), confirming the prediction of genetic organization of XALB1. The region upstream from operon 1 is 100 % identical to the region upstream from the *xabB* start codon which was described as a functional promoter during the phase of albicidin accumulation in Australian strain Xa13 of *X. albilineans* (Huang *et al.*, 2001). Involvement of several operons in albicidin biosynthesis suppose that they are transcribed during the same time. Promoter activities of regions upstream from putative operons 2, 3, 4 and 5 need to be determined to precise if these promoters are functional during the same growth phase of *X. albilineans* as the promoter upstream from operon 1.

Potential rho-independent transcription terminators were identified downstream from operons 1, 3 and 4 (Figure 6) confirming prediction of the genetic organization of these three operons. Because operons 2 and 5 are convergent (Figure 1) and separated by a very short region of 22 bp between *albIX* and *albXX*, stop codons may allow transcription termination in the absence of sequences corresponding to potential rho-independent transcription terminators downstream from these operons. It is quite possible that simultaneous transcription of

operons 2 and 5 involving the presence of two RNA polymerases (one on each strand of DNA) may cause RNA polymerases to pause at the end of each operon because of steric interference between both polymerase complexes in the same short region.

The presence of putative RBSs upstream of the ATG start codons of all ORFs, except for *albXVIII*, suggests that these ORFs are translated in *X. albilineans*. The absence of a canonical RBS upstream from *albXVIII* further indicates that this ORF is probably not expressed. GTG and TTG codons (usually valine and leucine codons) generally serve as procaryotic start codons when located near the 5' end of an RNA message, but GTG start codons were also described far from the 5' end of messenger RNA in the bacitracin biosynthesis cluster of *B. lucheniformis* (Genbank accession n° AF184956) or in the bleomycin biosynthetic gene cluster of *S. verticillus* (Genbank accession n° AF210249). This is in accordance with the fact that the two potential TTG start codons are the first start codons in operons 1 and 4 of XALB1, and that the two potential GTG start codons initiate internal cistrons. The *albI* and *albXVII* genes, like *xabB* (Huang *et al.*, 2001), use TTG as a start codon, which may impose post-transcriptional control of the rate of gene product formation (McCarthy and Gualerzi, 1990).

The predicted genetic organization of operons 1 and 2 presents similarities with the organization of the region involved in albicidin production in strain Xa13 of *X. albilineans* from Australia (Huang *et al.* 2000a, Huang *et al.*, 2001). This latter region also contains two divergent operons involved in albicidin production, one comprising the *xabB* gene (similar to *albI*, but with a large deletion) and the *xabC* gene (100% identical to *albII*) and the other containing *thp* gene (100% identical to *albV*). In addition, the sequence between the two operons in strain Xa13 is 100% identical to the sequence between operons 1 and 2, indicating that both clusters are controlled by the same bidirectional promoter. However, transposon mutagenesis studies of Xa13 showed no evidence of another cistron downstream of *xabC* that may be involved in albicidin production (Huang *et al.*, 2000a), suggesting that the Xa13 *xab* operon differs from the Xa23R1 operon 1, which contains two additional genes downstream from *albII* that are potentially involved in albicidin production (*albIII* and *albIV*; refer Figure 1).

Homology analysis revealed that four NRPS and/or PKS genes are present in XALB1 (Figure 2), and these genes may be involved in the biosynthesis of the albicidin polyketide-polypeptide backbone (*albI*, *albIV*, *albVII* and *albIX*). NRPS and PKS enzymes are generally organized into repeated functional units known as modules, each of which is responsible for a discrete stage of polyketide or polypeptide chain elongation (Cane and Walsh, 1999). Each

PKS or NRPS module is made up of a set of three core domains, two of which are catalytic and one of which acts as a carrier, and together are responsible for the central chain-building reactions of polyketide or polypeptide biosynthesis. Both PKS and NRPS core domains utilize analogous acyl-chain elongation strategies in which the growing chain, tethered as an acyl-S-enzyme to the flexible 20 Å long phosphopantetheinyl arm of an acyl carrier protein (ACP) or peptidyl carrier protein (PCP) domain, acts as the electrophilic partner that undergoes attack by a nucleophilic chain-elongation unit, a malonyl- or aminoacyl-S-enzyme derivative, respectively, itself covalently bound to a downstream ACP/PCP domain. In the case of a PKS, the fundamental chain-elongation reaction, a C-C bond-forming step, is mediated by a ketosynthase (KS) domain that catalyzes the transfer of the polyketide acyl chain to an active-site cysteine of the KS domain, followed by condensation with the methylmalonyl- or malonyl-S-ACP by a decarboxylative acylation of the malonyl donor unit. An additional essential component of the core PKS chain-elongation apparatus is an associated acetyltransferase (AT) domain, which catalyzes the priming of the donor ACP sidearm with the appropriate monomer substrate, usually methylmalonyl- or malonyl-CoA. The comparable core domains of an NRPS biosynthetic module function in a chemically distinct but architecturally and mechanistically analogous fashion. In the latter case, the key chain-building reaction, a C-N bond-forming reaction, involves the generation of the characteristic peptide bond by nucleophilic attack of the amino group of an amino acyl-S-PCP donor on the acyl group of an upstream electrophilic acyl- or peptidyl acyl-S-PCP chain, catalyzed by a condensation (C) domain. In functional analogy to the PKS AT domain, the core of the NRPS module utilizes an adenylation (A) domain to activate the donor amino-acid monomer as an acyl-AMP intermediate, which is then loaded onto the downstream PCP side chain. Both the AT and A domains of the respective PKS and NRPS modules act as important gatekeepers for polyketide or polypeptide biosynthesis, exhibiting strict or at least high specificity for their cognate malonyl-CoA, methylmalonyl-CoA or amino acid substrates. In addition to the basic subset of core domains, each PKS or NRPS also has a special set of dedicated domains responsible both for the initiation of acyl-chain assembly by loading of a starter unit onto the first, furthest upstream PKS/NRPS module, as well as a chain-terminating thioesterase (TE) domain, most often found fused to the last module, that is responsible for detachment of the most downstream covalent acyl enzyme intermediate and off-loading of the mature polyketide or polypeptide chain (Cane and Walsh, 1999).

XALB1 potentially encodes four PKS modules and seven NRPS modules. Most of the bacterial NRPS gene clusters described up to now are organized in operon-type structures,

encoding multi modular NRPS proteins with individual modules organized along the chromosome in a linear order that parallels the order of amino acids in the resultant peptide, following the "colinearity rule" for the NRPS-template assembly of peptides from amino acids (Cane, 1997; Cane *et al.*, 1998; Cane and Walsh, 1999; von Döhren *et al.*, 1999). PKS and NRPS modules are apparently not organized according to this "colinearity rule" for albicidin biosynthesis because of the following features : (I) NRPS and PKS genes are expressed in two divergent operons; (ii) no AT domain was identified in PKS-2 and PKS-3 domains, suggesting involvement of a separate enzyme ; (iii) the A domain of NRPS-2 is not functional, suggesting the involvement of a *trans*-acting A domain ; (iv) a single chain-terminating TE domain was identified in XALB1 which may be responsible of the release of the full length albicidin polyketide-polypeptide backbone from the enzyme complexes. Exception to the "colinearity rule" has also been shown for the syringomycin synthetase of *P. syringae* (Guenzi *et al.*, 1998), for the exochelin synthetase of *Mycobacterium smegmatis* (Yu *et al.*, 1998) and for the bleomycin synthetases of *S. verticillus* (Du *et al.*, 2000).

On the basis of the deduced functions of individual NRPS and PKS domains we have aligned the four PKS and the seven NRPS modules to suggest two different putative linear models for the synthesis of the albicidin polyketide-peptide backbone (Figure 9). In the Figure, NRPS and PKS domains are abbreviated as follows: A, adenylation; ACP, acyl carrier protein; AL, acyl-CoA ligase; AT, acyltransferase; C, condensation; HBCL,hydroxybenzoate-CoA ligase; KR, ketoreductase; KS, ketoacyl synthase; PCP, peptidyl carrier protein. Asn designates asparagine. X1 and X2 indicate substrates incorporated by NRPS -1 and 3 and by NRPS-6 and 7, respectively. The crossed A domain in NRPS-2 indicates that this deleted domain may be not functional. In model 1, (Figure 9A), (i) the PKS-1 module alone is responsible for the initiation of the acyl-chain assembly, (ii) PKS-4 (HBCL) interacts with PKS-2 and PKS-3 as an AT domain to allow acyl transfer and (iii) NRPS-5 interacts with only NRPS-2. In model 2 (Figure 9B) two different modules, PKS-1 and PKS-4, are responsible for this initiation step. Model 2 leads to the biosynthesis of four different polyketide-polypetide backbones; in this model (i) PKS-1 (AL) and PKS-4 (HBCL) are in competition for initiation of albicidin precursors; (ii) a separate AT enzyme (potentially AlbXIII) interacts with PKS-2 and PKS-3 to allow acyl transfer; (iii) NRPS-5 interacts with NRPS-2; and (iv) NRPS-5 and NRPS-6 are in competition for interaction with NRPS-4.

Both models are based on the fact that PKS-1 contains the AL and ACP1 domains, and PKS-4 shows homology with the hydroxybenzoate-CoA ligases. In other PKS systems, an N-terminal AL domain is involved in the activation and incorporation of an 3,4-dihydroxycyclo

hexane carboxylic acid, a 3-amino-5-hydroxybenzoic acid or a long-chain fatty acid as a starter (Aparicio *et al.*, 1996; Motamedi and Shafiee, 1998; Tang *et al.*, 1998; Duitman *et al.*, 1999). PKS-4 may be also involved in the activation and incorporation of hydroxy-benzoate but this latter domain lacks any ACP or PCP domain, suggesting that PKS-4 is responsible for initiation of the acyl-chain assembly (Figure 9B) onto one of the three ACP domains of AlbI (ACP1, ACP2 or ACP3). The 277 amino-acids preceding the PKS-4 module in AlbVII may be necessary for the intercommunication between AlbVII and AlbI. The presence of two different PKS modules potentially involved in the initiation of the acyl-chain assembly suggests a competition of these two modules for the initiation of two different albicidin polyketide-polypeptide backbones, and this could contribute to the production of multiple, structurally related albicidins by the same cluster XALB1. Production of two different components, one initiated by PKS-4 containing an additional aromatic ring due to incorporation of hydroxybenzoate, may explain why partial characterization of albicidin indicated the presence of a variable number (three or four) of aromatic rings (Huang *et al.*, 2001).

In AlbI, PKS-1 is followed by the PKS-2 module which contains a KS domain and a KR domain upstream from two ACP domains (ACP2 and ACP3) and it lacks any discernable AT domain. Tandem ACP domains are unusual within PKS modules but have been shown to occur in the biosynthesis of several fungal and bacterial polyketide synthases (Mayorga and Timberlake, 1992; Yu and Leonard, 1995; Takano *et al.*, 1995; Albertini *et al.*, 1995). However, the significance of the tandem ACP domains in these systems has not been solved yet. In our model 2, one of the tandem ACP (ACP2 or ACP3) may interact with PKS-4 for the initiation of an acyl-chain assembly (Figure 9B). The absence of an AT domain in the PKS-2 module suggests that a separate AT domain is indispensable for the elongation of the acyl-chain initiated by this module. Separate AT enzymes encoded elsewhere in the genome were described in other systems for two PKS modules lacking AT domains: malonyl-CoA transacyclase gene (*fen*F) located immediately upstream from the *B. subtilis* PKS-NRPS *mycA* gene (Duitman *et al.*, 1999) and an AT gene located 20kb upstream from the *M. xanthus* NRPS-PKS *tal* gene (Paitan *et al.*, 1999). We have not identified an AT gene in the gene cluster XALB1 and in the two other genomic regions involved in albicidin production, XALB2 and XALB3, suggesting that the *trans*-acting AT gene may be encoded elsewhere in the genome. However, AlbXIII, which contains the motif GHSxG conserved in AT domains, may be potentially involved in the acyl transfer, but the similarity of AlbXIII with AT domains is not high enough to confirm this potential function of AlbXIII (Figure 10). Figure

10A describes alignment of the conserved motifs in AT domains from RifA-1, -2, -3, RifB-1, RifE-1 (Rifamycin PKSs, August *et al.*, 1998) and BlmVIII (Bleomycin PKS; Du *et al.*, 2000), identical amino acids are shown in bold. Figure 10B describes alignment of AlbXIII (SEQ ID N°. 38), FenF (a malonyl-CoA transacylase located upstream from *mycA*, Duitman *et al.*,1999) and LipA (a lipase; Valdez *et al.*, 1999); amino acids identical to conserved AT domains motifs are shown in bold.

AlbXIII contains only four of the eleven amino acids conserved in AT domains of rifamycin PKSs (August *et al.*, 1998) and Bleomycin PKS (Du *et al.*, 2000), and the AlbXIII sequence appears to be more closely related to lipases such as LipA (Valdez *et al.*, 1999) rather than to AT domains (Figure 10). However, FenF, the *trans*-acting AT domain involved in mycosubtilin biosynthesis, contains only seven of the eleven amino acids conserved in AT domains (Duitman *et al.*, 1999; Figure 10). AlbVII, that contains a HBCL domain, may be another candidate for the acyl transfer in PKS-2 (Figure 9A) because HBCL exhibits some similarity with A domains at the level of cores A1, A2, A3, A4, A5 and A6 (Table 6). However, no HBCL involved in such a function has been described in the PKSs characterized so far.

In AlbI, PKS-2 is followed by the PKS-3 module which contains the KS2 and the PCP1 domains and it lacks any discernable AT or A domain. PKS-3 is located upstream from the NRPS modules and should therefore be involved in the linkage of polyketide and polypeptide moieties. The presence of a PCP domain in the PKS-3 module suggests the involvement of a *trans*-acting A domain rather than an AT domain. A putative candidate for this *trans*-acting A domain is the AlbIV NRPS-5 A domain because of the lack of a C domain in the AlbIV NRPS-5 module. However, by analogy with the BlmVIII PKS module, which is involved in the linkage of polypeptide and polyketide moieties of bleomycin and which contains an AT domain followed by a PCP domain (Du *et al*, 2000), the presence of a PCP is not incompatible with a possible interaction of the AlbI PKS-3 module with a separate AT domain. This latter *trans*-acting AT domain may be the same that interacts with the AlbI PKS-2 module, the AlbVII PKS-4 module, AlbXIII or an unindentified separate AT domain.

In AlbI, the PKS-3 module is followed by four NRPS modules. The NRPS-1, 2 and 3 modules display the ordered C, A and PCP domains, suggesting that they are involved in the incorporation of three amino acid residues. The A domain of the NRPS-2 module exhibits poor consensus at A2, A3, A5, A7, A8 A9 and A10 motifs and lacks completely the A6 motif (Table 6). In addition the NRPS-2 substrate binding pocket is partially deleted (Figure 5). These features strongly suggest that the NRPS-2 A domain is inactive and that the loading of

an amino-acid on the NRPS-2 PCP domain (PCP3) is possibly catalyzed by a *trans*-acting A domain as in HMWP1 (Gehring *et al.*, 1998) and BlmIII (Du *et al.*, 2000). A putative candidate for this *trans*-acting A domain is the NRPS-5 A domain present in AlbIV because of the lack of a C domain in NRPS-5 (Figure 2). The additional sequence of 300 amino-acids present in the A domain of NRPS-5 may be necessary for the intercommunication between AlbI and AlbIV. As a consequence of the interaction between NRPS-2 and NRPS-5, a competition between PCP-3 and PCP-5 domains must occur to bind the amino acid activated by the NRPS-5 A domain. A similar competition between two PCP domains was described for syringomycin biosynthesis, during the interaction between SyrB, which contains A and PCP domains, and the last module of SyrE which contains C and PCP domains (Guenzi *et al.*, 1998). The NRPS-4 module contains only a C domain which may transfer the intermediate products synthetized by AlbI to a PCP domain present in an other albicidin synthase. Similar transfers were described for mycosubtilin biosynthesis in which the MycA and MycB C-terminal C domains interact with the MycB and MycC N-terminal A domains, respectively (Duitman *et al.*, 1999). Two different PCP domains may be involved in the transfer of the intermediate products synthetized by AlbI: the PCP-5 and PCP-6 domains which are present in the AlbIV NRPS-5 and AlbIX NRPS-6 modules, respectively. This possible competition between the two NRPS modules that contain two different A domains could also contribute to the production of multiple, structurally related albicidins by the gene cluster XALB1 (Figure 9B). Because of the absence of a C-domain in the AlbIX NRPS-6 module, the intermediate product bound on the AlbIV PCP-5 domain would be necessarily transferred to the AlbIX PCP-7 domain, like the intermediate product bound on AlbIX PCP-6. AlbIX NRPS-7, which contains the single chain-terminating TE domain, may then be responsible for detachment of the mature albicidin polyketide-polypeptide backbone from the complex of enzymes.

The linear model 1 implies that operon 1 and operon 2 in *X. Albilineans* strain Xa23R1 from Florida potentially produce only one albicidin polyketide-polypetide backbone, with a competion at the level of ACP2/ACP3 and PCP3 and PCP5 which could explain the production by *X. albilineans* of compounds structurally related to albicidin (Figure 9A). The linear model 2 implies that operon 1 and operon 2 in *X. albilineans* strain Xa23R1 from Florida potentially produce four different albicidin polyketide-polypetide backbones (Figure 9B) because of (i) the competition of AL and HBCL domains for initation of acyl chain assembly and (ii) the competition of AlbIV NRPS-5 and AlbIX NRPS-6 modules for the incorporation of the next to last amino acid of the albicidin backbone. These four albicidin backbones may lead to the production of four components structurally very different. The

polyketide moieties of the acyl chains initiated by the AlbI AL domain or by the AlbVII HBCL domain may be very different. The polyketide moiety of acyl chains initiated by the AlbVII HBCL domain may be shorter and may contain an additional aromatic ring. The presence of four structuraly different metabolites may explain the difficulty observed by Birch and Patil (1985a) to purify albicidin and to determine its chemical structure.

Homology analysis also revealed that AlbI NRPS-1 and 3 and AlbIX NRPS-6 and 7 specify unusual substrates which seem to contain an amino group and a carboxylate group but to be different from α-amino acids and β-alanine. Identification of several aromatic rings in albicidin (Huang *et al* ., 2001) suggested that NRPS-1, -3, -6 and -7 are involved in incorporation of aromatic substrates. By analogy with the Asp235Val alteration in the β-Ala specificity-conferring code (Du *et al.* 2000), the Asp235Ala alteration in the NRPS-1, -3, -6 and -7 signatures could be consistent with a large distance between the amino group and the carboxylate group in the substrate specified by these modules. Based on this hypothesis, we suggest that operons 3, 4 and 5 are involved in the biosynthesis of two aromatic substrates: the para-aminobenzoate potentially synthesized by AlbXVII (para-aminobenzoate synthase), and the carbamoyl benzoate potentially synthesized by AlbXX (hydroxybenzoate synthase) and AlbXV (carbamoyl transferase). Incorporation of these nonproteinogenic substrates may explain why albicidin is insensitive to proteases (Birch and Patil, 1985a).

According to biosynthesis model 1 leading to the biosynthesis of only one polyketide-polypeptide albicidin backbone that may correspond to the major component produced by XAlb1, we propose a model allowing prediction of the composition and the structure of albicidin (Figure 11). In the Figure, NRPS and PKS domains are abbreviated as follows: A, adenylation; ACP, acyl carrier protein; AL, acyl-CoA ligase; C, condensation; KR, ketoreductase; KS, ketoacyl synthase; PCP, peptidyl carrier protein. C atoms of albicidin-backbone are numbered 1 to 38. Bold methyl groups correspond to methylation of the albicidin backbone by AlbII or AlbVI. In this model, albicidin biosynthesis is initiated by loading of an acetyl-CoA by PKS-1 (step 1), and the chain product is elongated by incorporation of (I) malonyl-CoA by PKS-2 and PKS-3 (steps 2 and 3), (ii) para-aminobenzoate or carbamoyl benzoate by NRPS-1 and NRPS-3 (steps 4 and 6), (iii) asparagine by NRPS-2 coupled to NRPS-5 (step 5) and (iv) para-aminobenzoate or carbamoyl benzoate by NRPS-6 and NRPS-7 (steps 7 and 8). The presence of the KR domain in the PKS-2 module may lead to the formation of an hydroxyl group at the C_2 atom of the albicidin backbone. This hydroxyl group might be methylated by AlbVI (*O*-methyltransferase). The acyl chain may also be modified by AlbII (*C*-methyltransferase) at C_{13} or C_{14}.

The chemical composition ($C_{40}O_{15}N_6H_{35}$), the molecular weight (839), and the structure of the putative XALB1 product are in accordance with the partial characterization of albicidin published by Birch and Patil (1985a) which indicated that albicidin contains approximately 38 carbon atoms and a carboxylate group and that the molecular weight of albicidin was about 842. The presence of two ester linkages in our predicted albicidin structure is also in accordance with the fact that albicidin is detoxified by the AlbD esterase (Zhang and Birch, 1997). However, an unpublished albicidin analysis cited by Huang *et al.* (2001) indicated the presence of (I) two OCH3 groups and not one as in our predictive albicidin structure, (ii) one CN linkage and not eleven as in our predictive albicidin structure and (iii) a trisubstituted double bond that is not present in the putative XALB1 product. Further investigations to identify the substrate of modules NRPS-1, 3, 6 and 7 and to characterize the structure of albicidin are necessary to valid our model for albicidin biosynthesis.

In conclusion, homology analysis of XALB1 revealed unprecedented features for hybrid polyketide-peptide biosynthesis in bacteria involving a *trans*-action of four PKS and seven NRPS separate modules which could contribute to the production of multiple, structurally related polyketide-peptide compounds by the same gene cluster. Characterization of the full chemical structure of albicidin may be necessary to validate these models. Four NRPS modules seem to activate a very unusual substrate. Over- expression and purification of A domains from these four NRPS modules will be necessary to examine their substrate specificities. Substrate specificity of each A domain will therefore be determinated by analysis of the ATP-PPi exchange reaction with different substrate putatively incorporated into albicidin. Investigating albicidin backbone biosynthesis will be of great interest because such information adds to the limited knowledge as to how PKS and NRPS interact and how they might be manipulated to engineer novel molecules, and may explain how *X. albilineans* produces several structurally related, toxic compounds.

Cloning and sequencing of XALB2 showed that the same phosphopantetheinyl transferase is required for albicidin production in an *X. albilineans* strain from Florida and in an *X. albilineans* strain from Australia (Huang *et al.*, 2000b), explaining the precedented results showing that strain LS156 mutated in *xabA* (100% identical to *albXXI*) was not complemented by pALB540, pALB571 and pALB639 (Rott *et al.*, 1996). Mutant LS156 was shown to be complemented by a construction containing the coding sequence of *xabA* in fusion with *lacZ*, revealing that *xabA* is required for albicidin production and that no other cistron downstream from *xabA* was involved in albicidin production (Huang *et al.*, 2000b).

However, this complementation study did not allow determination of whether *xabA* is transcribed as a part of a larger operon. Here we disclose the complementation of mutant AM37 with a 2986 bp insert from *X. albilineans* containing *albXXI* (100% identical to *xabA*), confirming that *albXXI* is involved in albicidin biosynthesis and indicating that the promoter of *albXXI* is present in the 2986 bp insert and that *albXXI* is not expressed as part of a operon.

Cloning and sequencing of XALB3 showed that a heat shock protein HtpG was involved in albicidin production in *X. albilineans*. The heat shock protein HtpG is an *Escherichia coli* homologue of eukaryotic HSP90 molecular chaperone. Hsp90 from eukaryotes has been demonstrated to possess chaperone activity (Jakob *et al.*, 1995), acting as a non-ATP dependent 'holder', and it also has an important role in signal transduction and the cell cycle. This protein is essential in both drosophila and yeast (Borkovich et al., 1989; Cutforth and Rubin, 1994). In contrast, the HtpG gene can be deleted in *E. coli* with no effect on the viability of the strain with the exception of decreased growth rate at high temperatures (Bardwell and Craig, 1988). The *in vivo* role of the HtpG protein remains unknown. However, preliminary results indicated that HtpG facilitates *de novo* protein folding in stressed *E. coli* cells, presumably by expanding the ability of the DnaK-DnaJ-GrpE molecular chaperone system to interact with newly synthesized polypeptides (Thomas and Baneyx, 2000). Furthermore, HtpG was copurified in *E. coli* with MccB17 synthetase, an enzyme involved in the biosynthesis of the peptide antibiotic microcin B17 which inhibits DNA replication by induction of the SOS repair system, suggesting the requirement of HtpG for production of the antibiotic (Li *et al.*, 1996). However, when microcin B17 production by the *E. coli* strain deleted for HtpG was compared to the one of the parental strain, there was no effect on microcin B17 production *in vivo*. This result implyed that the copurification of HtpG with the MccB17 synthetase was potentially an artefact, or that another *E. coli* chaperone could substitute for HtpG (Milne *et al.*, 1999). To examine the effect of HtpG on the reconstitution of MccB17 synthetase *in vitro*, the chaperone was expressed and purified as a fusion to a hexahistidine (His_6) tag. Addition of the His_6-HtpG did not stimulate MccB17 synthetase reconstitution or heterocyclisation activity *in vitro*, suggesting that HtpG mediates complex assembly or stabilizes protein subunits prior to the hetero-oligomerisation (Milne *et al.*, 1999). Based on these results, we suggest that the function of AlbXXII is to mediate complex assembly by facilitating *de novo* protein folding of PKS and NRPS enzymes (AlbI, AlbIV, AlbVII and AlbIX) involved in the albicidin backbone biosynthesis.

Characterization of the complete sequence of XALB1, XALB2 and XALB3 clusters enables one to characterize all enzymes of the albicidin biosynthesis pathway including

structural, resistance, secretory and regulatory elements, and to engineer overproduction of albicidin. For example one may insert expression enhancing DNA into the genome of *X. albilineans* in a position operable to enhance expression of the Albicidins Biosynthesis Gene Clusters. One may also modify naturally occurring Albicidins to obtain additional non-naturally occurring antibiotics by adding DNA encoding additional enzymes selected to produce a modified albicidin like molecule. This approach will allow (I) the purification of albicidin and the other compounds structurally related and potentially produced by the same biosynthesis apparatus; (ii) the characterization of chemical structure of albicidin; (iii) the investigation of mode of action of albicidin in the pathogenesis of *X. albilineans* in sugarcane; and (iv) the characterization of the bactericidal activity of albicidin. For example one may also increase the resistance of plants to damage from *X. albilineans* infection by inserting one or more of the resistance genes identified herein into the genome of the plant. One may also provide materials to prevent damage by albicidin produced by *X. albilineans* by applying an agent that blocks expression of the Albicidin Biosynthesis Gene Clusters to the plant to be protected. One may also use portions of the DNA of the Albicidin Biosynthesis Gene Clusters to obtain agents useful in blocking expression of albicidin by screening materials against a modified hast cell line that expresses the Albicidin Biosynthesis Gene Clusters and selecting for materials that stop or decrease albicidin production.

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tgccttttgc aactggatga gcaagaacat gtgctgctaa tcggcatgca tcaccttatc 19740

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<213> Xanthomonas albilineans

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ggcagcatca agttcctgct ctcgccctac atcatgagcg ccttcaccga tctgaccgcc 360

gtagtcagga ccggcaagat caacctggcg caggacggcg tggtggcacc ggatcacccg 420

cagtgggtgg aatttgcacg cgcgatggca ccgatgatgg cgctgccctc ggcgttgatc 480

gccaatatgg tgtcgttgcc cgctgatcgg ccgattcgtg tgctggacgt ggcagccggc 540

cacggcctgt tcggcatcgc cttcgcgcag cgcttccgcc aggctgaagt gagcttcctg 600

gactgggaca acgtgctaga cgtagcacgc gaaaacgccc aggcggccaa agtggccgag 660

cgagcgcgtt tcctgcccgg caacgcattc gacctcgatt acggcagcgg ctacgacgtg 720

atcttgttga ccaacttcct gcaccatttc gatgaggtcg atggcgagcg catcttggct 780

aagacgcgcg atgcgctgaa cgacgacggc atggtgatca ctttcgaatt catcgccgac 840

gaagagcgtt cctcaccgcc gctggccgcc accttcagca tgatgatgct gggcaccacc 900

ccggcgggcg agtcctacac ctatagcgat ctggaaagga tgtttcggca tgccggcttc 960

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agggccccat aa 1032

<210> 22
<211> 504
<212> DNA
<213> Xanthomonas albilineans

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atgatcgaga tcggctcgga ctatctggtc tcctgcatgt cggtggactg gcgttgccac 180

cagccctatg gggtattgca tggcggcgca tcggtcaccc tggccgaggc taccggcagc 240

atggcggcct ccatgtgcgt gccggccggc caacgttgcg ttggcctaga catcaatgcc 300

aaccacatcg cgagcatctc cagtggccaa gtacagtgca tcgcgcggcc gctgcacata 360

ggggccttga cccaggtatg gcagatgcgc atctatgacg aaggtgaccg cacgatctgc 420

gtgtcgcgcc tgaccatggc ggtattatcg gtgcacgtcg cgcgcgtatc cccgaatcca 480

gccagcagcg gagtccagac gtga 504

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<211> 2826
<212> DNA
<213> Xanthomonas albilineans

<400> 23
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gcataa 2826

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<213> Xanthomonas albilineans

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gtcggacgct acttcgactt cagcgcggca cgcctgtgcg gcatcgacct ggcacggcaa 720

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<210> 25
<211> 1905
<212> DNA
<213> Xanthomonas albilineans

<400> 25
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cgcaagtact ccgaccacat cgccttgccg atcgagctaa tcaaggaaca ctacggcgag 660

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<210> 26
<211> 6879
<212> PRT
<213> Xanthomonas albilineans

<400> 26

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Gly Val Leu Leu Gly Val Thr Ala Arg Ala Ala Ile Pro Asn Lys Ala
            20                  25                  30

Gly Met Arg Arg Ala Trp Pro Pro Phe Pro Gln Ala Cys Cys Arg Ser
        35                  40                  45

Ile Ala Tyr Leu Met Gln Arg Ser Pro Met Ser Pro Leu Gln Gln Thr
    50                  55                  60

Leu Leu Thr Arg Leu Ala Ser Ala Ala Ala Ser Arg Thr Met Ile Glu
65                  70                  75                  80

Phe Pro Arg Pro Glu His Ala Ser Pro Gln Cys Cys Asp Asp Ala Glu
                85                  90                  95

Leu Ala Arg Leu Ile Val Gln Leu Ser Ala Gly Leu Gln Pro Leu Ala
            100                 105                 110

Met Pro Gly Thr Tyr Val Ile Ile Ala Ala Pro His Gly Gly Leu Phe
        115                 120                 125

Ala Ala Ala Leu Leu Ala Cys Leu His Ala Asn Leu Val Ala Val Pro
    130                 135                 140

Phe Pro Leu Asp Val Ala Gln Pro Asn Glu Arg Glu Gln Ala Arg Leu
145                 150                 155                 160

Glu Thr Ile His Ala Gln Leu Met Glu His Gly Asn Val Ala Val Leu
```

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                    165                 170                 175

Leu Asp Asp Val Ala Asp Arg Ser Ala Phe Ala Arg Met Ala His Ala
             180                 185                 190

Ala Gly Thr Phe Leu Ala Thr Phe Ala Asp Leu Lys Arg Glu Ser Thr
        195                 200                 205

Ser Ala Ser Leu Cys Pro Ala Ser Pro Ser Asp Ala Ala Leu Leu Leu
    210                 215                 220

Phe Thr Ser Gly Ser Ser Gly Glu Ser Lys Gly Ile Leu Leu Ser His
225                 230                 235                 240

Arg Asn Leu His His Gln Ile Gln Ala Gly Ile Arg Gln Trp Ser Leu
                245                 250                 255

Asp Glu His Ser His Val Val Thr Trp Leu Ser Pro Ala His Asn Phe
            260                 265                 270

Gly Leu His Phe Gly Leu Leu Ala Pro Trp Phe Ser Gly Ala Thr Val
        275                 280                 285

Ser Phe Ile His Pro His Ser Tyr Met Lys Arg Pro Gly Phe Trp Leu
    290                 295                 300

Glu Thr Val Ala Ala Arg Asp Ala Thr His Met Ala Ala Pro Asn Phe
305                 310                 315                 320

Ala Phe Asp Tyr Cys Cys Asp Trp Val Met Val Glu Gln Leu Pro Pro
                325                 330                 335
```

```
Ser Ala Leu Ser Thr Leu Thr His Ile Val Cys Gly Gly Glu Pro Val
            340                 345                 350

Arg Ala Ser Thr Met Gln Arg Phe Phe Glu Lys Phe Ala Gly Leu Gly
        355                 360                 365

Ala Arg Thr Gln Thr Phe Met Pro His Phe Gly Leu Ser Glu Thr Gly
    370                 375                 380

Ala Leu Ser Thr Leu Asp Glu Ala Pro Gln Gln Arg Val Leu Glu Leu
385                 390                 395                 400

Asp Ala Asp Ala Leu Asn Lys Arg Lys Arg Val Ala Ala Gly Ala Ser
                405                 410                 415

Gln Ala Arg Val Thr Val Leu Asn Cys Gly Ala Val Asp Gln Asp Val
            420                 425                 430

Glu Leu Arg Ile Val Cys Pro Glu Gly Glu Thr Leu Cys Arg Pro Asp
        435                 440                 445

Glu Ile Gly Glu Ile Trp Val Lys Ser Pro Ala Ile Ala Arg Gly Tyr
    450                 455                 460

Leu Phe Ala Lys Pro Ala Asp Gln Arg Gln Phe Asn Cys Ser Ile Arg
465                 470                 475                 480

His Thr Asp Asp Ser Gly Tyr Phe Arg Thr Gly Asp Leu Gly Phe Ile
                485                 490                 495
```

```
Ala Asp Gly Cys Leu Tyr Val Thr Gly Arg Val Lys Glu Val Leu Ile
            500                 505                 510

Ile Arg Gly Lys Asn His Tyr Pro Ala His Ile Glu Ala Ser Ile Ala
        515                 520                 525

Ala Thr Ala Ser Pro Gly Ala Leu Met Pro Val Val Phe Ser Ile Glu
    530                 535                 540

Arg Gln Asp Glu Glu Arg Val Ala Ala Val Ile Ala Val Asn His Pro
545                 550                 555                 560

Trp Thr Pro Ala Ala Cys Ala Ala Gln Ala His Lys Ile Arg Gln Gln
                565                 570                 575

Val Ala Asp Gln His Gly Val Ala Leu Ala Glu Leu Ala Phe Ala Glu
            580                 585                 590

His Arg His Val Phe Gly Thr Tyr Pro Gly Lys Leu Lys Arg Arg Leu
        595                 600                 605

Val Lys Glu Ala Tyr Val Asn Gly Gln Leu Pro Leu Leu Trp His Glu
    610                 615                 620

Gly Lys Asn Arg Asp Val Pro Ala Ala Ala Ala Asp Asp Arg Gln Ala
625                 630                 635                 640

Gln His Val Ala Asp Leu Cys Arg Lys Val Phe Leu Pro Val Leu Gly
                645                 650                 655

Val Ala Pro Pro His Ala Gln Trp Pro Leu Cys Glu Leu Ala Leu Asp
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660 665 670

Ser Leu Gln Cys Val Arg Leu Ala Gly Ala Ile Glu Glu Cys Tyr Gly
675 680 685

Val Pro Phe Glu Pro Thr Leu Leu Phe Lys Leu Glu Thr Val Gly Ala
690 695 700

Ile Ala Glu Tyr Val Leu Ala His Gly Arg Gln Ala Pro Thr Pro Thr
705 710 715 720

Arg Ala Pro Val Ala Ser Thr Thr Cys Ser Glu Glu Pro Ile Ala Ile
725 730 735

Val Ala Met His Cys Glu Val Pro Gly Ala Gly Glu Asn Thr Glu Ala
740 745 750

Leu Trp Ser Phe Leu Arg Ser Asp Val Asn Ala Ile Arg Pro Ile Glu
755 760 765

Ser Thr Arg Pro Asp Leu Trp Ala Ala Met Arg Ala Tyr Pro Gly Leu
770 775 780

Ala Gly Glu Gln Leu Pro Arg Tyr Ala Gly Phe Leu Asp Asp Val Asp
785 790 795 800

Ala Phe Asp Ala Ala Phe Phe Gly Ile Ser Arg Arg Glu Ala Glu Cys
805 810 815

Met Asp Pro Gln Gln Arg Lys Val Leu Glu Met Val Trp Lys Leu Ile
820 825 830

```
Glu Gln Ala Gly His Asp Pro Leu Ser Trp Gly Gly Gln Pro Val Gly
        835                 840                 845

Leu Phe Val Gly Ala His Thr Ser Asp Tyr Gly Glu Leu Leu Ala Ser
    850                 855                 860

Gln Pro Gln Leu Met Ala Gln Cys Gly Ala Tyr Ile Asp Ser Gly Ser
865                 870                 875                 880

His Leu Thr Met Ile Pro Asn Arg Ala Ser Arg Trp Phe Asn Phe Thr
                885                 890                 895

Gly Pro Ser Glu Val Ile Asn Ser Ala Cys Ser Ser Ser Leu Val Ala
            900                 905                 910

Leu His Arg Ala Val Gln Ser Leu Arg Gln Gly Glu Ser Ser Val Ala
        915                 920                 925

Leu Val Leu Gly Val Asn Leu Ile Leu Ala Pro Lys Val Leu Leu Ala
    930                 935                 940

Ser Ala Ser Ala Gly Met Leu Ser Pro Asp Gly Arg Cys Lys Thr Leu
945                 950                 955                 960

Asp Ala Ala Ala Asp Gly Phe Val Arg Ser Glu Gly Ile Ala Gly Val
                965                 970                 975

Ile Leu Lys Pro Leu Ala Gln Ala Leu Ala Asp Gly Asp Arg Val Tyr
            980                 985                 990
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Gly Leu Val Arg Gly Val Ala Val Asn His Gly Gly Arg Ser Asn Ser
995 1000 1005

Leu Arg Ala Pro Asn Val Asn Ala Gln Arg Gln Leu Leu Ile Arg
1010 1015 1020

Thr Tyr Gln Glu Ala Gly Val Glu Pro Ala Ser Val Gly Tyr Val
1025 1030 1035

Glu Leu His Gly Thr Gly Thr Ser Leu Gly Asp Pro Ile Glu Ile
1040 1045 1050

Gln Ala Leu Lys Glu Ala Phe Ile Ala Leu Gly Ala Gln Ala Ala
1055 1060 1065

Pro Ser Asn Cys Gly Ile Gly Ser Val Lys Ser Ala Leu Gly His
1070 1075 1080

Leu Glu Ala Ala Ala Gly Leu Thr Gly Leu Ile Lys Val Leu Leu
1085 1090 1095

Met Leu Lys His Gly Glu Gln Ala Gly Thr Arg His Phe Ser Thr
1100 1105 1110

Leu Asn Pro Leu Ile Asp Leu Arg Gly Thr Ser Phe Glu Val Val
1115 1120 1125

Ala Gln His Arg Ala Trp Pro Ser Gln Val Gly Ile His Gly Thr
1130 1135 1140

Leu Leu Pro Arg Arg Ala Gly Ile Ser Ser Phe Gly Phe Gly Gly

```
1145                1150                1155

Ala Asn Ala His Ala Ile Val Glu Glu His Val Ile Ala Thr Pro
1160                1165                1170

Pro Ser Thr Ser Ser Ala Gly Gly Pro Val Gly Ile Val Leu Ser
1175                1180                1185

Ala Gly Ser Glu Ala Val Leu Arg Gln Gln Val Leu Ala Leu Ser
1190                1195                1200

Ala Trp Leu Arg Gln Gln Ser Pro Thr Pro Ala Gln Met Ile Asp
1205                1210                1215

Val Ala Tyr Thr Leu Gln Val Gly Arg Ala Ala Leu Ser His Arg
1220                1225                1230

Leu Ala Phe Ser Ala Thr Asp Ala Glu Gln Ala Leu Ala Arg Leu
1235                1240                1245

Glu Gly Arg Leu Ala Gly Val Met Asp Ala Glu Val His His Gly
1250                1255                1260

Val Val Asp Ala Ala Ala Thr Ala Pro Glu His Gly Arg Gln Thr
1265                1270                1275

Arg Glu Gly Leu Ala Gly Leu Leu Arg Ala Trp Thr Gln Gly Val
1280                1285                1290

Arg Val Asp Trp Ser Ala Leu Tyr Gly Ile Gln Arg Pro Gln Arg
1295                1300                1305
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Val Ser  Leu Pro Val Tyr Pro  Phe Ala Arg Glu Arg  Tyr Trp Leu
    1310                 1315                 1320

Pro Gly  Gln Ala Met His Ala  Ala Ala Asp Ala His  Pro Met Leu
    1325                 1330                 1335

Gln Leu  Leu His Ala Asn Ala  Lys Leu His Arg Tyr  Ala Leu Arg
    1340                 1345                 1350

Arg Ser  Gly Cys Ala Ser Phe  Leu Val Asp His Cys  Val Asp Gly
    1355                 1360                 1365

Arg Gln  Val Leu Pro Ala Ala  Val Gln Leu Glu Leu  Val Arg Ala
    1370                 1375                 1380

Val Ala  Gln Arg Val Met Ala  Gln Asp Glu Gly Cys  Ile Glu Leu
    1385                 1390                 1395

Ala Gln  Val Ala Phe Leu His  Pro Leu Met Met Glu  Glu Thr Glu
    1400                 1405                 1410

Leu Glu  Val Glu Ile Glu Leu  Ser Lys Ser Asp Gln  Asp Glu Phe
    1415                 1420                 1425

Asp Phe  Gln Leu His Asp Ala  His Arg Gln Gln Val  Phe Ser Gln
    1430                 1435                 1440

Gly His  Val Arg Arg Arg Val  Tyr Thr Ala Thr Pro  Arg Leu Asp
    1445                 1450                 1455
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Leu Ala Gln Leu Gln Lys Leu Cys Ala Glu Arg Val Leu Ser Gly
1460 1465 1470

Glu Asp Cys Tyr Ala His Phe Thr Ala Cys Gly Leu Gln Leu Gly
1475 1480 1485

Asp Arg Leu Lys Ser Val Gln Ser Ile Gly Cys Gly Arg Asn Gly
1490 1495 1500

Glu Gly Glu Pro Ile Ala Leu Gly Val Leu Arg Leu Pro Pro Ser
1505 1510 1515

Ser Val Glu Asp Ser His Val Leu Pro Pro Ser Leu Leu Asp Gly
1520 1525 1530

Ala Leu Gln Cys Ser Leu Gly Leu Gln Arg Asp Val Glu His Ile
1535 1540 1545

Ala Met Pro Tyr Thr Leu Glu Arg Met Thr Val His Ala Pro Ile
1550 1555 1560

Pro Pro Glu Ala Trp Val Leu Leu Arg His Gly His Ala Ala Arg
1565 1570 1575

Gln Ser Leu Asp Ile Asp Leu Leu Asp Ser Glu Gly Arg Val Cys
1580 1585 1590

Val Ser Leu Gly Asn Tyr Thr Gly Arg Ala Pro Lys Ala Val Ser
1595 1600 1605

Ala Val Arg Ala Leu Val Leu Ala Pro Val Trp Gln Ala Leu Thr

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1610                1615                1620

Glu Thr Ala Pro Ala Trp Pro Asp Pro Ala Glu Arg Ile Val Thr
1625                1630                1635

Val Gly Asp Asp Ala Trp Arg Ser His Phe Gly Phe Asp Glu Pro
1640                1645                1650

Ala Leu Ser Leu Glu Asp Ser Val Glu Val Ile Ala Thr Arg Leu
1655                1660                1665

Gly Gln Ser Gly Lys Phe Asp His Leu Val Trp Ile Val Pro Ile
1670                1675                1680

Ala Glu Ser Glu Thr Asp Ile Ala Ala Gln Gly Ser Ala Ala Ile
1685                1690                1695

Ala Gly Phe Arg Leu Val Lys Ala Leu Leu Ala Leu Gly Tyr Ala
1700                1705                1710

His Arg Pro Leu Gly Leu Thr Val Leu Thr Arg Gln Ala Leu Thr
1715                1720                1725

Arg Gln Pro Ser His Ala Ala Val His Gly Leu Ile Gly Thr Leu
1730                1735                1740

Ala Lys Glu Tyr Cys Asn Trp Lys Ile Arg Leu Leu Asp Leu Pro
1745                1750                1755

Ser Val Lys Ser Trp Pro Gln Trp Glu Gln Leu Arg Ser Leu Pro
1760                1765                1770
```

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Trp His  Ala Gln Gly Glu Ala  Leu Ile Gly Arg Gly  Thr Cys Trp
    1775                 1780                 1785

Tyr Arg  Arg Gln Leu Cys Glu  Val Leu Pro Leu Pro  Ser Leu Glu
    1790                 1795                 1800

Pro Pro  Pro Tyr Arg Val Gly  Gly Val Tyr Val Val  Ile Gly Gly
    1805                 1810                 1815

Ala Gly  Gly Leu Gly Glu Val  Leu Ser Glu His Leu  Ile Arg Thr
    1820                 1825                 1830

Tyr Asp  Ala Gln Leu Ile Trp  Ile Gly Arg Arg Val  Leu Asp Glu
    1835                 1840                 1845

Gly Ile  Ala Arg Lys Gln Thr  Arg Leu Ala Ser Leu  Gly Arg Ala
    1850                 1855                 1860

Pro His  Tyr Ile Ser Ala Asp  Ala Ser Asp Pro Ala  Ala Leu Gln
    1865                 1870                 1875

Ala Ala  His Asn Glu Ile Val  Ala Leu His Gly Gln  Pro His Gly
    1880                 1885                 1890

Leu Ile  Leu Ser Asn Ile Val  Leu Lys Asp Ala Ser  Leu Ala Arg
    1895                 1900                 1905

Met Glu  Glu Ala Asp Phe Arg  Asp Val Leu Ala Ala  Lys Leu Asp
    1910                 1915                 1920
```

Val Ser Val Cys Ala Ala Gln Val Phe Gly Thr Ala Pro Leu Asp
1925 1930 1935

Phe Val Leu Phe Phe Ser Ser Ile Gln Ser Thr Thr Lys Ala Ala
1940 1945 1950

Gly Gln Gly Asn Tyr Ala Ala Gly Cys Cys Tyr Val Asp Ala Phe
1955 1960 1965

Gly Glu Leu Trp Ala Arg Arg Gly Leu Arg Val Lys Thr Ile Asn
1970 1975 1980

Trp Gly Tyr Trp Gly Ser Val Gly Val Val Ala Gly Glu Asp Tyr
1985 1990 1995

Arg Arg Arg Met Ala Gln Lys His Met Ala Ser Ile Glu Gly Ala
2000 2005 2010

Glu Ala Met Gln Val Leu Ser Gln Leu Leu Cys Ala Pro Leu Gln
2015 2020 2025

Arg Leu Ala Tyr Val Lys Ile Asp Asp Ala Asn Ala Met Arg Ala
2030 2035 2040

Leu Gly Val Val Glu Asp Glu Ser Val Gln Ile Pro Val His Ala
2045 2050 2055

Pro Ala Glu Pro Pro Arg Gly Gln Pro Gly Pro Val Val Glu Leu
2060 2065 2070

Ser Val Asn Leu Asp Ala Arg Arg Glu Arg Glu Thr Leu Leu Ala

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    2075                2080                2085

Ala Trp  Leu Leu Glu Leu Ile  Glu Gln Leu Gly Gly  Phe Pro Pro
    2090                2095                2100

Ala Ser  Phe Asp Ile Ala Thr  Leu Ala Gln Arg Leu  His Ile Val
    2105                2110                2115

Pro Ala  Tyr Arg Ser Trp Leu  Glu His Ser Val Arg  Met Leu Gly
    2120                2125                2130

Val Tyr  Gly Tyr Leu Arg Ala  Thr Gly Glu Ser Arg  Phe Glu Leu
    2135                2140                2145

Ala Asp  Lys Pro Pro Asp Asp  Ala Arg Gly Ala Trp  Asn Ala His
    2150                2155                2160

Val His  Glu Ala Ser Val Glu  Ala Gly Glu Glu Ala  Gln Arg Arg
    2165                2170                2175

Leu Leu  Asp Arg Cys Met Arg  Ala Leu Pro Ala Val  Leu Arg Gly
    2180                2185                2190

Glu Arg  Lys Ala Thr Glu Leu  Leu Phe Pro Glu Gly  Ser Met Ala
    2195                2200                2205

Trp Val  Glu Gly Ile Tyr Gln  Asn Asn Pro Leu Ala  Asp Tyr Phe
    2210                2215                2220

Asn Ala  Gln Leu Val Thr Arg  Leu Ile Ala Tyr Leu  Arg Arg Arg
    2225                2230                2235
```

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Leu Glu  Ser Thr Pro Thr Ala  Arg Leu Lys Leu Cys  Glu Ile Gly
    2240                  2245                  2250

Ala Gly  Ser Gly Gly Thr Thr  Ala Ser Val Leu Gln  Gln Leu Gln
    2255                  2260                  2265

Ala Tyr  Gly Glu His Ile Glu  Glu Tyr Leu Tyr Thr  Asp Leu Ser
    2270                  2275                  2280

Pro Val  Phe Leu His His Ala  Glu Lys His Tyr Gln  Pro Arg Ala
    2285                  2290                  2295

Pro Tyr  Leu Arg Thr Ala Cys  Phe Asp Val Ala Arg  Ala Pro Thr
    2300                  2305                  2310

Ala Gln  Ala Leu Glu Ser Gly  Gly Tyr Asp Val Val  Ile Ala Ala
    2315                  2320                  2325

Asn Val  Leu His Ala Thr Arg  Asp Ile Ala Lys Thr  Leu Arg Asn
    2330                  2335                  2340

Ala Lys  Ala Leu Leu Lys Pro  Gly Gly Leu Leu Leu  Leu Asn Glu
    2345                  2350                  2355

Val Ile  Glu Arg Ser Leu Val  Leu His Leu Thr Phe  Gly Leu Leu
    2360                  2365                  2370

Glu Ser  Trp Trp Leu Pro Gln  Asp Lys Ile Leu Arg  Leu Ala Gly
    2375                  2380                  2385
```

```
Ser Pro  Leu Leu Ala Cys Ala  Thr Trp Arg Ser Leu  Leu Glu Ala
    2390                 2395                 2400

Glu Gly  Phe Ala Gly Leu Ser  Val His Arg Ala Gln  Pro Asp Ala
    2405                 2410                 2415

Gly Gln  Ala Ile Ile Cys Ala  Tyr Ser Asp Gly Ile  Val Arg Gln
    2420                 2425                 2430

Ala Ser  Thr Ile Glu Val Ala  Arg Asn Glu Lys Val  Thr Val Pro
    2435                 2440                 2445

Ser Gln  Pro Ala Glu Ala Gly  Glu Ser Pro Leu Asp  Leu Val Lys
    2450                 2455                 2460

Lys Leu  Leu Gly Arg Ile Leu  Lys Met Asp Pro Ala  Thr Leu Asp
    2465                 2470                 2475

Thr Ser  His Pro Leu Glu Tyr  Tyr Gly Val Asp Ser  Ile Val Ala
    2480                 2485                 2490

Ile Glu  Leu Ala Met Ala Leu  Arg Glu Thr Phe Pro  Gly Phe Glu
    2495                 2500                 2505

Val Ser  Glu Leu Phe Glu Thr  Gln Ser Ile Asp Thr  Leu Leu Gly
    2510                 2515                 2520

Ser Leu  Glu Gln Ala Pro Leu  Leu Ala Thr Leu Thr  Ala Pro Pro
    2525                 2530                 2535

Gln Gln  Asp Met Leu Gln Gln  Leu Lys Gln Leu Leu  Ala Arg Thr
```

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    2540                2545                2550

Leu Lys  Leu Asp Ile Thr Gln  Ile Asp Thr Ser Lys  Thr Leu Glu
    2555                2560                2565

Ser Tyr  Gly Val Asp Ser Ile  Val Ile Ile Glu Leu  Ala Asn Ala
    2570                2575                2580

Leu Arg  Glu Arg Tyr Pro Ser  Leu Asp Ala Ser Gln  Leu Met Glu
    2585                2590                2595

Thr Leu  Ser Ile Asp Arg Leu  Val Ala Gln Trp Gln  Ala Thr Glu
    2600                2605                2610

Pro Ala  Val Pro Ala Glu Pro  Thr Ala Glu Pro Pro  Val Ala Asp
    2615                2620                2625

Glu Asp  Ala Ala Ala Ile Ile  Gly Leu Ala Gly Arg  Phe Pro Gly
    2630                2635                2640

Ala Asp  Thr Leu Glu Glu Phe  Trp Asn Asn Leu Arg  Asn Gly Gln
    2645                2650                2655

Ser Ser  Met Gly Glu Val Pro  Gly Glu Arg Trp Asp  His Gln His
    2660                2665                2670

Tyr Phe  Asp Ser Glu Arg Gln  Ala Pro Gly Lys Thr  Tyr Ser Arg
    2675                2680                2685

Trp Gly  Ala Phe Leu Arg Asp  Ile Asp Gly Phe Asp  Ala Ala Phe
    2690                2695                2700
```

```
Phe Glu  Trp Pro Asp Ser Val  Ala Leu Glu Ser Asp  Pro Gln Ala
    2705                 2710                 2715

Arg Ile  Phe Leu Glu Gln Ala  Tyr Ala Gly Ile Glu  Asp Ala Gly
    2720                 2725                 2730

Tyr Thr  Pro Gly Ser Leu Ser  Lys Ser Gln Arg Val  Gly Val Phe
    2735                 2740                 2745

Val Gly  Val Met Asn Gly Tyr  Tyr Ser Gly Gly Ala  Arg Phe Trp
    2750                 2755                 2760

Gln Ile  Ala Asn Arg Val Ser  Tyr Gln Phe Asp Phe  Arg Gly Pro
    2765                 2770                 2775

Ser Leu  Ala Val Asp Thr Ala  Cys Ser Ala Ser Leu  Thr Ala Ile
    2780                 2785                 2790

His Leu  Ala Leu Glu Ser Leu  Arg Ser Gly Ser Cys  Glu Val Ala
    2795                 2800                 2805

Leu Ala  Gly Gly Val Asn Leu  Leu Val Asp Pro Gln  Gln Tyr Leu
    2810                 2815                 2820

Asn Leu  Ala Gly Ala Ala Met  Leu Ser Ala Gly Ala  Ser Cys Arg
    2825                 2830                 2835

Pro Phe  Gly Glu Ala Ala Asp  Gly Phe Val Ala Gly  Glu Ala Cys
    2840                 2845                 2850
```

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Gly Val  Val Leu Leu Lys Pro  Leu Lys Gln Ala Arg  Ala Asp Gly
    2855                 2860                 2865

Asp Val  Ile His Ala Val Ile  Arg Gly Ser Met Ile  Asn Ala Gly
    2870                 2875                 2880

Gly His  Thr Ser Ala Phe Ser  Ser Pro Asn Pro Ala  Ala Gln Ala
    2885                 2890                 2895

Glu Val  Val Arg Gln Ala Leu  Gln Arg Ala Gly Val  Ala Pro Asp
    2900                 2905                 2910

Ser Ile  Ser Tyr Ile Glu Ala  His Gly Thr Gly Thr  Val Leu Gly
    2915                 2920                 2925

Asp Ala  Val Glu Leu Gly Ala  Leu Asn Lys Val Phe  Asp Lys Arg
    2930                 2935                 2940

Ala Ala  Pro Cys Pro Ile Gly  Ser Leu Lys Ala Asn  Ile Gly His
    2945                 2950                 2955

Ala Glu  Ser Ala Ala Gly Ile  Ala Gly Leu Ala Lys  Leu Val Leu
    2960                 2965                 2970

Gln Phe  Arg His Gly Glu Leu  Val Pro Ser Leu Asn  Ala Phe Pro
    2975                 2980                 2985

Leu Asn  Pro Tyr Ile Glu Phe  Gly Arg Phe Gln Val  Gln Gln Gln
    2990                 2995                 3000

Pro Ala  Pro Trp Pro Arg Arg  Gly Ala Gln Pro Arg  Arg Ala Gly
```

3005 3010 3015

Leu Ser Ala Phe Gly Ala Gly Gly Ser Asn Ala His Leu Val Val
3020 3025 3030

Glu Glu Ala Pro Ala Met Ala Pro Gly Val Ser Ile Ser Ala Ser
3035 3040 3045

Ser Pro Ala Leu Ile Val Leu Ser Ala Arg Thr Leu Pro Ala Leu
3050 3055 3060

Gln Gln Arg Ala Arg Asp Leu Leu Val Trp Met Gln Ala Arg Gln
3065 3070 3075

Val Asp Asp Val Met Leu Ala Asp Val Ala Tyr Thr Leu His Leu
3080 3085 3090

Gly Arg Val Ala Met Glu Gln Arg Leu Ala Phe Thr Ala Gly Ser
3095 3100 3105

Ala Ala Glu Leu Ser Glu Lys Leu Gln Ala Tyr Leu Gly His Ala
3110 3115 3120

Ile Arg Ala Asp Ile Tyr Leu Ser Glu Asp Thr Pro Gly Lys Pro
3125 3130 3135

Ala Gly Ala Pro Ile Val Ala Glu Glu Asp Leu Leu Thr Leu Met
3140 3145 3150

Asp Ala Trp Ile Glu Lys Gly Gln Tyr Gly Arg Leu Leu Glu Tyr
3155 3160 3165

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Trp Thr  Lys Gly Gln Pro Ile  Asp Trp Asn Lys Leu  Tyr Trp Arg
    3170                 3175                 3180

Lys Leu  Tyr Ala Asp Gly Arg  Pro Arg Arg Ile Ser  Leu Pro Thr
    3185                 3190                 3195

Tyr Pro  Phe Glu His Arg Arg  Tyr Trp Gln Thr Pro  Val Pro Gly
    3200                 3205                 3210

Glu Arg  Ser Leu His Ala Thr  Ala Pro Ala Thr Arg  Glu Thr Val
    3215                 3220                 3225

Ala Val  Gly Ala Met Pro Asp  Pro Ala Gly Ala Thr  Val Gln Ala
    3230                 3235                 3240

Arg Leu  Cys Ala Leu Cys Gln  Val Leu Leu Gly Lys  Pro Val Thr
    3245                 3250                 3255

Ala Gln  Met Asp Phe Phe Ala  Val Gly Gly His Ser  Val Leu Ala
    3260                 3265                 3270

Ile Gln  Leu Val Ser Arg Ile  Arg Lys Ser Phe Gly  Val Glu Tyr
    3275                 3280                 3285

Pro Val  Ser Ala Leu Phe Glu  Ser Ala Leu Leu Ser  Asp Met Ala
    3290                 3295                 3300

Arg Gln  Ile Glu Gln Leu Arg  Val Asn Gly Val Ala  Lys Arg Met
    3305                 3310                 3315
```

Pro Ala Leu Leu Pro Ala Gly Arg Val Gly Ala Ile Pro Ala Thr
3320 3325 3330

Tyr Ala Gln Glu Arg Leu Trp Leu Val His Glu His Met Ser Glu
3335 3340 3345

Gln Arg Ser Ser Tyr Asn Ile Thr Phe Ala Met His Phe Arg Gly
3350 3355 3360

Val Asp Phe Arg Ala Glu Ala Met Arg Ala Ala Leu Asn Ala Leu
3365 3370 3375

Val Val Arg His Glu Val Leu Arg Thr Arg Phe Leu Ser Glu Asp
3380 3385 3390

Gly Gln Leu Gln Gln Val Ile Ala Ala Ser Leu Thr Leu Glu Val
3395 3400 3405

Pro Val Arg Glu Met Ser Val Glu Glu Val Asp Leu Leu Leu Ala
3410 3415 3420

Ala Ser Thr Arg Glu Thr Phe Asp Leu Arg Gln Gly Pro Leu Phe
3425 3430 3435

Lys Ala Arg Ile Leu Arg Val Ala Ala Asp His His Val Val Leu
3440 3445 3450

Ser Ser Ile His His Ile Ile Ser Asp Gly Trp Ser Leu Gly Val
3455 3460 3465

Phe Asn Arg Asp Leu His Gln Leu Tyr Glu Ala Cys Leu Arg Gly

3470 3475 3480

Thr Pro Pro Thr Leu Pro Thr Leu Ala Val Gln Tyr Ala Asp Tyr
3485 3490 3495

Ala Leu Trp Gln Arg Gln Trp Glu Leu Ala Ala Pro Leu Ser Tyr
3500 3505 3510

Trp Thr Arg Ala Leu Glu Gly Tyr Asp Asp Gly Leu Asp Leu Pro
3515 3520 3525

Tyr Asp Arg Pro Arg Gly Ala Thr Arg Ala Trp Arg Ala Gly Leu
3530 3535 3540

Val Lys His Arg Tyr Pro Pro Gln Leu Ala Gln Gln Leu Ala Ala
3545 3550 3555

Tyr Ser Gln Gln Tyr Gln Ala Thr Leu Phe Met Ser Leu Leu Ala
3560 3565 3570

Gly Leu Ala Leu Val Leu Gly Arg Tyr Ala Asp Arg Lys Asp Val
3575 3580 3585

Cys Ile Gly Ala Thr Val Ser Gly Arg Asp Gln Leu Glu Leu Glu
3590 3595 3600

Glu Leu Ile Gly Phe Phe Ile Asn Ile Leu Pro Leu Arg Val Asp
3605 3610 3615

Leu Ser Gly Asp Pro Cys Leu Glu Glu Val Leu Leu Arg Thr Arg
3620 3625 3630

Gln Val Val Leu Asp Gly Phe Ala His Gln Ser Val Pro Phe Glu
3635 3640 3645

His Val Leu Gln Ala Leu Arg Arg Gln Arg Asp Ser Ser Gln Ile
3650 3655 3660

Pro Leu Val Pro Val Met Leu Arg His Gln Asn Phe Pro Thr Gln
3665 3670 3675

Glu Ile Gly Asp Trp Pro Glu Gly Val Arg Leu Thr Gln Met Glu
3680 3685 3690

Leu Gly Leu Asp Arg Ser Thr Pro Ser Glu Leu Asp Trp Gln Phe
3695 3700 3705

Tyr Gly Asp Gly Ser Ser Leu Glu Leu Thr Leu Glu Tyr Ala Gln
3710 3715 3720

Asp Leu Phe Asp Glu Ala Thr Val Arg Arg Met Ile Ala His His
3725 3730 3735

Gln Gln Ala Leu Glu Ala Met Val Ser Arg Pro Gln Leu Arg Val
3740 3745 3750

Gly Lys Trp Asp Met Leu Thr Ala Glu Glu Arg Arg Leu Phe Ala
3755 3760 3765

Ala Leu Asn Ala Thr Gly Thr Pro Arg Glu Trp Pro Ser Leu Ala
3770 3775 3780

```
Gln Gln  Phe Glu Arg Gln Ala  Gln Ala Thr Pro Gln  Ala Ile Ala
    3785                 3790                 3795

Cys Val  Ser Asp Gly Gln Ser  Trp Ser Tyr Ala Gln  Leu Glu Ala
    3800                 3805                 3810

Arg Ala  Asn Gln Leu Ala Gln  Ala Leu Arg Gly Gln  Gly Ala Gly
    3815                 3820                 3825

Arg Asp  Val Arg Val Ala Val  Gln Ser Ala Arg Thr  Pro Glu Leu
    3830                 3835                 3840

Leu Met  Ala Leu Leu Ala Ile  Phe Lys Ala Gly Ala  Cys Tyr Val
    3845                 3850                 3855

Pro Ile  Asp Pro Ala Tyr Pro  Ala Ala Tyr Arg Glu  Gln Ile Leu
    3860                 3865                 3870

Ala Glu  Val Gln Val Ser Ile  Val Leu Glu Gln Asp  Glu Leu Ala
    3875                 3880                 3885

Leu Asp  Glu Gln Gly Gln Phe  His Asn Pro Arg Trp  Arg Glu Gln
    3890                 3895                 3900

Ala Pro  Thr Pro Leu Gly Leu  Arg Glu His Pro Gly  Asp Leu Ala
    3905                 3910                 3915

Cys Val  Met Val Thr Ser Gly  Ser Thr Gly Arg Pro  Lys Gly Val
    3920                 3925                 3930

Met Val  Pro Tyr Ala Gln Leu  Tyr Asn Trp Leu His  Ala Gly Trp
```

3935 3940 3945

Gln Arg Ser Pro Phe Glu Ala Gly Glu Arg Val Leu Gln Lys Thr
3950 3955 3960

Ser Ile Ala Phe Ala Val Ser Val Lys Glu Leu Leu Ser Gly Leu
3965 3970 3975

Leu Ala Gly Val Glu Gln Val Met Leu Pro Asp Glu Gln Val Lys
3980 3985 3990

Asp Ser Leu Ala Leu Ala Arg Ala Ile Glu Gln Trp Gln Val Thr
3995 4000 4005

Arg Leu Tyr Leu Val Pro Ser His Leu Gln Ala Leu Leu Asp Ala
4010 4015 4020

Thr Gln Gly Arg Asp Gly Leu Leu His Ser Leu Arg His Val Val
4025 4030 4035

Thr Ala Gly Glu Ala Leu Pro Ser Ala Val Arg Glu Thr Val Arg
4040 4045 4050

Ala Arg Leu Pro Gln Val Gln Leu Trp Asn Asn Tyr Gly Cys Thr
4055 4060 4065

Glu Leu Asn Asp Ala Thr Tyr His Arg Ser Asp Thr Val Ala Pro
4070 4075 4080

Gly Thr Phe Val Pro Ile Gly Ala Pro Ile Ala Asn Thr Glu Val
4085 4090 4095

Tyr Val Leu Asp Arg Gln Leu Arg Gln Val Pro Ile Gly Val Met
4100 4105 4110

Gly Glu Leu His Val His Ser Val Gly Met Ala Arg Gly Tyr Trp
4115 4120 4125

Asn Arg Pro Gly Leu Thr Ala Ser Arg Phe Ile Ala His Pro Tyr
4130 4135 4140

Ser Glu Glu Pro Gly Thr Arg Leu Tyr Lys Thr Gly Asp Met Val
4145 4150 4155

Arg Arg Leu Ala Asp Gly Thr Leu Glu Tyr Leu Gly Arg Gln Asp
4160 4165 4170

Phe Glu Val Lys Val Arg Gly His Arg Val Asp Thr Arg Gln Val
4175 4180 4185

Glu Ala Ala Leu Arg Ala Gln Pro Ala Val Ala Glu Ala Val Val
4190 4195 4200

Ser Gly His Arg Val Asp Gly Asp Met Gln Leu Val Ala Tyr Val
4205 4210 4215

Val Ala Arg Glu Gly Gln Ala Pro Ser Ala Gly Glu Leu Lys Gln
4220 4225 4230

Gln Leu Ser Ala Gln Leu Pro Thr Tyr Met Leu Pro Thr Val Tyr
4235 4240 4245

```
Gln Trp  Leu Glu Gln Leu Pro  Arg Leu Ser Asn Gly  Lys Leu Asp
    4250                 4255                 4260

Arg Leu  Ala Leu Pro Ala Pro  Gln Ala Val His Ala  Gln Glu Tyr
    4265                 4270                 4275

Val Ala  Pro Arg Asn Gln Ala  Glu Gln Arg Leu Ala  Ala Leu Phe
    4280                 4285                 4290

Ala Glu  Val Leu Arg Val Glu  Gln Val Gly Ile His  Asp Asn Phe
    4295                 4300                 4305

Phe Ala  Leu Gly Gly His Ser  Leu Ser Ala Ser Gln  Leu Ile Ser
    4310                 4315                 4320

Arg Ile  Ala Arg Asp Met Ala  Ile Asp Leu Pro Leu  Ala Met Leu
    4325                 4330                 4335

Phe Glu  Leu Pro Thr Val Ala  Gln Leu Ser Glu Ser  Leu Ala Ser
    4340                 4345                 4350

His Ala  Arg Asp Ser Asp Tyr  Asp Val Ile Pro Ala  Ser Thr Glu
    4355                 4360                 4365

Glu Ala  Thr Ile Pro Leu Ser  Thr Ala Gln Glu Arg  Met Trp Phe
    4370                 4375                 4380

Leu His  Lys Phe Val Gln Glu  Thr Pro Tyr Asn Thr  Pro Gly Leu
    4385                 4390                 4395

Ala Leu  Leu Gln Gly Glu Leu  Asp Ile Ser Ala Leu  Gln Val Ala
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4400                4405                4410

Phe Arg  Cys Val Leu Glu Arg  His Ala Val Leu Arg  Thr His Phe
4415                4420                4425

Val Glu  Thr Glu Gln Gln Cys  Val Gln Val Ile Gly  Ala Ala Glu
4430                4435                4440

Gln Phe  Val Leu Gln Leu Arg  Ser Ile Arg Asp Glu  Ala Asp Leu
4445                4450                4455

His Gly  Leu Leu His Thr Ala  Val Ser Glu Pro Phe  Asp Leu Glu
4460                4465                4470

Arg Glu  Leu Pro Leu Arg Ala  Leu Leu Tyr Arg Leu  Asp Asp Arg
4475                4480                4485

Arg His  Tyr Leu Ala Val Val  Ile His His Ile Val  Phe Asp Gly
4490                4495                4500

Trp Ser  Thr Ser Ile Leu Phe  Arg Glu Leu Ala Thr  His Tyr Ala
4505                4510                4515

Ala Cys  Arg His Gly Gln Ser  Ala Pro Leu Pro Pro  Leu Glu Leu
4520                4525                4530

Ser Tyr  Ala Asp Tyr Ala Arg  Trp Glu Arg Ala Arg  Leu Asn Gln
4535                4540                4545

Glu Asp  Ala Leu Arg Lys Leu  Glu Tyr Trp Lys Thr  Gln Leu Ala
4550                4555                4560
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```
Asp Ala  Pro Pro Leu Val Leu  Pro Thr Thr Tyr Ala  Arg Pro Val
    4565                 4570                 4575

Phe Gln  Asn Phe Asn Gly Ala  Thr Val Ala Leu Gln  Ile Glu Pro
    4580                 4585                 4590

Pro Leu  Leu Gln Arg Leu Gln  Arg Phe Ala Asp Ala  His Ser Phe
    4595                 4600                 4605

Thr Leu  Tyr Met Leu Leu Leu  Ala Ala Leu Gly Val  Val Leu Ser
    4610                 4615                 4620

Arg His  Ala Arg Gln Lys His  Phe Cys Ile Gly Ser  Pro Val Ala
    4625                 4630                 4635

Asn Arg  Ala Arg Ala Glu Leu  His Gly Leu Ile Gly  Leu Phe Val
    4640                 4645                 4650

Asn Thr  Leu Ala Val Arg Leu  Asp Leu Asp Gly Asn  Pro Ser Val
    4655                 4660                 4665

Arg Glu  Leu Leu Glu Arg Ile  His Cys Thr Thr Leu  Ala Ala Tyr
    4670                 4675                 4680

Glu His  Gln Asp Val Pro Phe  Glu Arg Ile Val Glu  Ser Leu Lys
    4685                 4690                 4695

Val Pro  Arg Asp Thr Ala Arg  Asn Pro Leu Gly Gln  Val Met Leu
    4700                 4705                 4710
```

Asn Phe Gln Asn Met Pro Met Ser Ala Phe Asp Leu Asp Gly Val
4715 4720 4725

Gln Val Gln Val Leu Pro Met His Asn Gly Thr Ala Lys Cys Glu
4730 4735 4740

Leu Thr Phe Asp Leu Leu Leu Asp Gly Ser Arg Leu Ser Gly Phe
4745 4750 4755

Val Glu Tyr Ala Thr Gly Leu Phe Ala Pro Glu Trp Val Gln Ala
4760 4765 4770

Leu Val Gln Gln Phe Lys Cys Val Leu Ala Ala Leu Val Glu Arg
4775 4780 4785

Pro Glu Ala Ser Leu Asn Asp Leu Pro Met Ala Pro Asn Glu Ala
4790 4795 4800

Gln Pro Ala Ser Pro Ala Leu Met Lys His Val Ala Pro Ser Leu
4805 4810 4815

Pro Asn Leu Leu Glu Ala Met Ala Ala Asn Asp Ala Ala Arg Leu
4820 4825 4830

Ala Leu Gln Ala Pro Glu Gly Ala Leu Ser Tyr Ala Gln Leu Ile
4835 4840 4845

Glu Ala Ala Asn Glu Phe Ala Trp Arg Leu Arg Cys Glu His Ala
4850 4855 4860

Gly Pro Asp Lys Val Val Ala Leu Cys Leu Ala Pro Cys Ser Ala

4865 4870 4875

Leu Val Val Ala Leu Leu Ala Ala Ser Leu Cys Gly Ala Ala Ser
4880 4885 4890

Val Leu Ile Asp Pro Thr Thr Thr Ala Glu Ala Gln Tyr Asp Gln
4895 4900 4905

Leu Phe Glu Thr Arg Ala Gly Ile Val Val Thr Cys Ser Ser Leu
4910 4915 4920

Leu Glu Lys Leu Pro Leu Asp Asp Gln Ala Val Val Leu Ile Asp
4925 4930 4935

Glu Gln Ala Ala Glu Ala Thr Pro Arg Leu Met His Phe Thr Asp
4940 4945 4950

Asp Pro Ala Leu Pro Ala Met Leu Tyr Cys Val Cys Asp Glu Lys
4955 4960 4965

Gly Arg Thr Arg Thr Ile Met Val Glu Ser Gly Ser Leu Ser Ser
4970 4975 4980

Arg Leu Leu Asp Ser Val Gln Arg Phe Ser Leu Glu Arg Thr Asp
4985 4990 4995

Arg Phe Leu Leu Arg Ser Pro Leu Ser Ala Glu Leu Ala Asn Thr
5000 5005 5010

Glu Val Leu Gln Trp Leu Ala Ala Gly Gly Ser Leu Ser Ile Ala
5015 5020 5025

```
Pro Met  His Gly Asp Phe Asp  Ala Ala Ala Trp Leu  Glu Thr Leu
    5030                 5035                 5040

Ala Thr  Tyr Ala Ile Thr Val  Ala Tyr Leu Ala Gln  Val Glu Leu
    5045                 5050                 5055

Thr Glu  Met Leu Ala His Leu  Gln Asn His Pro Leu  Glu Arg Asn
    5060                 5065                 5070

Lys Leu  Ala Gly Leu Arg Val  Leu Val Val His Gly  Ala Pro Leu
    5075                 5080                 5085

Pro Ile  Ala Pro Leu Met Arg  Leu Asp Ala Trp Leu  Arg Glu Val
    5090                 5095                 5100

Gly Gly  Ser Ala Arg Ile Phe  Ala Ala Tyr Gly Asn  Ala Glu Phe
    5105                 5110                 5115

Gly Ala  Glu Ile Leu Ser Gln  Asp Val Ser Ala Ala  Leu Gln Ala
    5120                 5125                 5130

Gly Ile  Gly Ala Gln Tyr Lys  His Arg Arg Gly Leu  Phe Pro Leu
    5135                 5140                 5145

Gly Ala  Asn Ser Met Cys His  Val Val Gln Ser Asn  Gly Arg Ile
    5150                 5155                 5160

Ala Pro  Asp Gly Met Val Gly  Glu Leu Trp Ile Thr  Gln Pro Ala
    5165                 5170                 5175
```

```
Cys Leu  Tyr Lys Thr Asp Ala  Leu Val Arg Arg Leu  Ala Asn Gly
    5180                 5185                 5190

Gln Leu  Glu Trp Leu Gly Ser  Leu Asp Val Gln Ser  Arg Ile Asp
    5195                 5200                 5205

Asp Pro  Arg Ile Asp Leu Cys  Val Val Glu Ala Gln  Leu Arg Leu
    5210                 5215                 5220

Cys Glu  Asp Val Gly Glu Ala  Val Val Leu Tyr Glu  Pro Leu Lys
    5225                 5230                 5235

Arg Cys  Leu Val Ala Tyr Leu  Ser Ala Arg Ser Thr  Ala Ala Ile
    5240                 5245                 5250

Met Thr  Asp Glu Thr Leu Ala  Arg Ile Arg Gln Ala  Leu Ser Glu
    5255                 5260                 5265

Thr Leu  Pro Asp Tyr Leu Leu  Pro Ala Ile Trp Val  Pro Leu Ala
    5270                 5275                 5280

His Trp  Pro Arg Leu Pro His  Gly Arg Val Asp Leu  Gly Ala Leu
    5285                 5290                 5295

Pro Ala  Pro Asp Phe Asp Leu  Ala Arg His Glu Ser  Tyr Ile Ala
    5300                 5305                 5310

Pro Arg  Thr Ala Val Glu Gln  Ala Val Ala Glu Ile  Trp Gln Arg
    5315                 5320                 5325

Val Leu  Lys Arg Thr Gln Val  Gly Val His Asp Asn  Phe Phe Glu
```

5330 5335 5340

Leu Gly Gly His Ser Val Leu Ala Ile Gln Leu Val Ser Gly Leu
5345 5350 5355

Arg Lys Ala Leu Ala Ile Glu Val Pro Val Thr Leu Val Phe Glu
5360 5365 5370

Ala Pro Ile Leu Gly Ala Leu Ala Arg Gln Ile Ala Pro Leu Leu
5375 5380 5385

Val Ser Glu Arg Arg Pro Arg Pro Pro Gly Leu Thr Arg Leu Glu
5390 5395 5400

His Thr Gly Pro Ile Pro Ala Ser Tyr Ala Gln Glu Arg Leu Trp
5405 5410 5415

Leu Val His Glu His Met Glu Glu Gln Arg Thr Ser Tyr Asn Ile
5420 5425 5430

Ser Asn Ala Ala His Phe Ile Gly Ala Ala Phe Ser Val Glu Ala
5435 5440 5445

Met Arg Ala Ala Leu Asn Ala Leu Val Ala Arg His Glu Val Leu
5450 5455 5460

Arg Thr Arg Phe Leu Ser Glu Asp Gly Gln Leu Gln Gln Val Ile
5465 5470 5475

Ala Ala Ser Leu Thr Leu Glu Val Pro Val Arg Glu Val Ser Ala
5480 5485 5490

```
Glu Glu  Val Asp Leu Leu Leu  Ala Ala Ser Thr Arg  Glu Thr Phe
    5495                 5500                 5505

Asp Leu  Arg Gln Gly Pro Leu  Phe Lys Ala Arg Ile  Leu Arg Val
    5510                 5515                 5520

Ala Ala  Asp His His Val Val  Leu Ser Ser Ile His  His Ile Ile
    5525                 5530                 5535

Ser Asp  Gly Trp Ser Leu Gly  Val Phe Asn Arg Asp  Leu His Gln
    5540                 5545                 5550

Leu Tyr  Glu Ala Cys Leu Arg  Gly Thr Pro Pro Thr  Leu Pro Thr
    5555                 5560                 5565

Leu Ala  Val Gln Tyr Ala Asp  Tyr Ala Leu Trp Gln  Arg Gln Trp
    5570                 5575                 5580

Glu Leu  Ala Ala Pro Leu Ser  Tyr Trp Thr Arg Ala  Leu Glu Gly
    5585                 5590                 5595

Tyr Asp  Asp Gly Leu Asp Leu  Pro Tyr Asp Arg Pro  Arg Gly Ala
    5600                 5605                 5610

Thr Arg  Ala Trp Arg Ala Gly  Leu Val Lys His Arg  Tyr Pro Pro
    5615                 5620                 5625

Gln Leu  Ala Gln Gln Leu Ala  Ala Tyr Ser Gln Gln  Tyr Gln Ala
    5630                 5635                 5640
```

```
Thr Leu  Phe Met Ser Leu Leu  Ala Gly Leu Ala Leu  Val Leu Gly
    5645                 5650                 5655

Arg Tyr  Ala Asp Arg Lys Asp  Val Cys Ile Gly Ala  Thr Val Ser
    5660                 5665                 5670

Gly Arg  Asp Gln Leu Glu Leu  Glu Glu Leu Ile Gly  Phe Phe Ile
    5675                 5680                 5685

Asn Ile  Leu Pro Leu Arg Val  Asp Leu Ser Gly Asp  Pro Cys Leu
    5690                 5695                 5700

Glu Glu  Val Leu Leu Arg Thr  Arg Gln Val Val Leu  Asp Gly Phe
    5705                 5710                 5715

Ala His  Gln Ser Val Pro Phe  Glu His Val Leu Gln  Ala Leu Arg
    5720                 5725                 5730

Arg Gln  Arg Asp Ser Ser Gln  Ile Pro Leu Val Pro  Val Met Leu
    5735                 5740                 5745

Arg His  Gln Asn Phe Pro Thr  Gln Glu Ile Gly Asp  Trp Pro Glu
    5750                 5755                 5760

Gly Val  Arg Leu Thr Gln Met  Glu Leu Gly Leu Asp  Arg Ser Thr
    5765                 5770                 5775

Pro Ser  Glu Leu Asp Trp Gln  Phe Tyr Gly Asp Gly  Ser Ser Leu
    5780                 5785                 5790

Glu Leu  Thr Leu Glu Tyr Ala  Gln Asp Leu Phe Asp  Glu Ala Thr
```

5795 5800 5805

Val Arg Arg Met Ile Ala His His Gln Gln Ala Leu Glu Ala Met
5810 5815 5820

Val Ser Arg Pro Gln Leu Arg Val Gly Lys Trp Asp Met Leu Thr
5825 5830 5835

Ala Glu Glu Arg Arg Leu Phe Ala Ala Leu Asn Ala Thr Gly Thr
5840 5845 5850

Pro Arg Glu Trp Pro Ser Leu Ala Gln Gln Phe Glu Arg Gln Ala
5855 5860 5865

Gln Ala Thr Pro Gln Ala Ile Ala Cys Val Ser Asp Gly Gln Ser
5870 5875 5880

Trp Ser Tyr Ala Gln Leu Glu Ala Arg Ala Asn Gln Leu Ala Gln
5885 5890 5895

Ala Leu Arg Gly Gln Gly Ala Gly Arg Asp Val Arg Val Ala Val
5900 5905 5910

Gln Ser Ala Arg Thr Pro Glu Leu Leu Met Ala Leu Leu Ala Ile
5915 5920 5925

Phe Lys Ala Gly Ala Cys Tyr Val Pro Ile Asp Pro Ala Tyr Pro
5930 5935 5940

Ala Ala Tyr Arg Glu Gln Ile Leu Ala Glu Val Gln Val Ser Ile
5945 5950 5955

```
Val Leu  Glu Gln Gly Glu Leu  Ala Leu Asp Glu Gln  Gly Gln Phe
    5960                 5965                 5970

Arg Asn  Arg Arg Trp Arg Glu  Gln Ala Pro Thr Pro  Leu Gly Leu
    5975                 5980                 5985

Arg Gly  His Pro Gly Asp Leu  Ala Cys Val Met Val  Thr Ser Gly
    5990                 5995                 6000

Ser Thr  Gly Arg Pro Lys Gly  Val Met Val Pro Tyr  Ala Gln Leu
    6005                 6010                 6015

His Asn  Trp Leu His Ala Gly  Trp Gln Arg Ser Ala  Phe Glu Ala
    6020                 6025                 6030

Gly Glu  Arg Val Leu Gln Lys  Thr Ser Ile Ala Phe  Ala Val Ser
    6035                 6040                 6045

Val Lys  Glu Leu Leu Ser Gly  Leu Leu Ala Gly Val  Gly Gln Val
    6050                 6055                 6060

Met Leu  Pro Asp Glu Gln Val  Lys Asp Ser Leu Ala  Leu Ala Arg
    6065                 6070                 6075

Ala Ile  Glu Gln Trp Gln Val  Thr Arg Leu Tyr Leu  Val Pro Ser
    6080                 6085                 6090

His Leu  Gln Ala Leu Leu Asp  Ala Thr Gln Gly Arg  Asp Gly Leu
    6095                 6100                 6105
```

Leu His Ser Leu Arg His Val Val Thr Ala Gly Glu Ala Leu Pro
6110 6115 6120

Ser Ala Val Gly Glu Ala Val Arg Val Arg Leu Pro Gln Val Gln
6125 6130 6135

Leu Trp Asn Asn Tyr Gly Cys Thr Glu Leu Asn Asp Ala Thr Tyr
6140 6145 6150

His Arg Ser Asp Thr Val Ala Pro Gly Thr Phe Val Pro Ile Gly
6155 6160 6165

Ala Pro Ile Ala Asn Thr Glu Val Tyr Val Leu Asp Arg Gln Leu
6170 6175 6180

Arg Gln Val Pro Ile Gly Val Met Gly Glu Leu His Val His Ser
6185 6190 6195

Val Gly Met Ala Arg Gly Tyr Trp Asn Arg Pro Gly Leu Thr Ala
6200 6205 6210

Ser Arg Phe Ile Ala His Pro Tyr Ser Glu Glu Pro Gly Thr Arg
6215 6220 6225

Leu Tyr Lys Thr Gly Asp Met Val Arg Arg Leu Ala Asp Gly Thr
6230 6235 6240

Leu Glu Tyr Leu Gly Arg Gln Asp Phe Glu Val Lys Val Arg Gly
6245 6250 6255

His Arg Val Asp Thr Arg Gln Val Glu Ala Ala Leu Arg Ala Gln

```
     6260                6265                6270

Pro Ala  Val Ala Glu Ala Val  Val Ser Gly His Arg  Val Asp Gly
     6275                6280                6285

Asp Met  Gln Leu Val Ala Tyr  Val Val Ala Arg Glu  Gly Gln Ala
     6290                6295                6300

Pro Ser  Ala Gly Glu Leu Lys  Gln Gln Leu Ser Ala  Gln Leu Pro
     6305                6310                6315

Thr Tyr  Met Leu Pro Thr Val  Tyr Gln Trp Leu Glu  Gln Leu Pro
     6320                6325                6330

Arg Leu  Ser Asn Gly Lys Leu  Asp Arg Leu Ala Leu  Pro Ala Pro
     6335                6340                6345

Gln Val  Val His Ala Gln Glu  Tyr Val Ala Pro Arg  Asn Glu Ala
     6350                6355                6360

Glu Gln  Arg Leu Ala Ala Leu  Phe Ala Glu Val Leu  Arg Val Glu
     6365                6370                6375

Gln Val  Gly Ile His Asp Asn  Phe Phe Ala Leu Gly  Gly His Ser
     6380                6385                6390

Leu Ser  Ala Ser Gln Leu Ile  Ser Arg Ile Arg Gln  Ser Phe His
     6395                6400                6405

Val Asp  Leu Pro Leu Ser Arg  Ile Phe Glu Ala Pro  Thr Ile Glu
     6410                6415                6420
```

Gly Leu Val Arg Gln Leu Ala Leu Pro Ser Glu Gly Gly Val Ala
6425 6430 6435

Ser Ile Ala Arg Val Ala Arg Asn Arg Thr Ile Pro Leu Ser Leu
6440 6445 6450

Phe Gln Glu Arg Leu Trp Phe Val His Gln His Met Pro Glu Gln
6455 6460 6465

Arg Thr Ser Tyr Asn Gly Thr Leu Ala Leu Arg Leu Arg Gly Pro
6470 6475 6480

Leu Ser Val Glu Ala Met Arg Ala Ala Leu Arg Ala Leu Val Leu
6485 6490 6495

Arg His Glu Ile Leu Arg Thr Arg Phe Val Leu Pro Thr Gly Ala
6500 6505 6510

Ser Glu Pro Val Gln Val Ile Asp Glu His Ser Asp Phe Gln Leu
6515 6520 6525

Ser Val Gln Leu Val Glu Asp Thr Glu Ile Ala Ser Leu Met Asp
6530 6535 6540

Glu Leu Ala Ser His Ile Tyr Asp Leu Ala Asn Gly Pro Leu Phe
6545 6550 6555

Ile Ala Cys Leu Leu Gln Leu Asp Glu Gln Glu His Val Leu Leu
6560 6565 6570

Ile Gly Met His His Leu Ile Tyr Asp Ala Trp Ser Gln Phe Thr
6575 6580 6585

Val Met Asn Arg Asp Leu Arg Val Leu Tyr His Arg His Leu Gly
6590 6595 6600

Leu Ala Gly Gly Asp Leu Pro Glu Leu Pro Ile Gln Tyr Ala Asp
6605 6610 6615

Tyr Ala Ile Trp Gln Arg Ala Gln Asn Leu Asp Ala Gln Leu Ala
6620 6625 6630

Tyr Trp Gln Ala Met Leu His Asp Tyr Asp Asp Gly Leu Glu Leu
6635 6640 6645

Pro Tyr Asp Tyr Pro Arg Pro Arg Asn Arg Thr Trp His Ala Ala
6650 6655 6660

Val Tyr Thr His Thr Tyr Pro Ala Glu Leu Val Gln Arg Phe Ala
6665 6670 6675

Gly Phe Val Gln Ala His Gln Ser Thr Leu Phe Ile Gly Leu Leu
6680 6685 6690

Ala Ser Phe Ala Val Val Leu Asn Lys Tyr Thr Gly Arg Asp Asp
6695 6700 6705

Leu Cys Ile Gly Thr Thr Thr Ala Gly Arg Thr His Leu Glu Leu
6710 6715 6720

Glu Asn Leu Ile Gly Phe Phe Ile Asn Ile Leu Pro Leu Arg Leu

6725 6730 6735

Arg Leu Asp Gly Asp Pro Asp Val Ala Glu Ile Met Arg Arg Thr
6740 6745 6750

Arg Leu Val Ala Met Ser Ala Phe Glu Asn Gln Ala Leu Pro Phe
6755 6760 6765

Glu His Leu Leu Asn Ala Leu His Lys Gln Arg Asp Thr Ser Arg
6770 6775 6780

Ile Pro Leu Val Pro Val Val Met Arg His Gln Asn Phe Pro Asp
6785 6790 6795

Thr Ile Gly Asp Trp Ser Asp Gly Ile Arg Thr Glu Val Ile Gln
6800 6805 6810

Arg Asp Leu Arg Ala Thr Pro Asn Glu Met Asp Leu Gln Phe Phe
6815 6820 6825

Gly Asp Gly Thr Gly Leu Ser Val Thr Val Glu Tyr Ala Ala Glu
6830 6835 6840

Leu Phe Ser Glu Ala Thr Ile Arg Arg Leu Ile His His His Gln
6845 6850 6855

Leu Val Leu Glu Gln Met Leu Ala Ala His Glu Ser Ala Thr Cys
6860 6865 6870

Pro Leu Asp Val Ala Asp
6875

<210> 27
<211> 343
<212> PRT
<213> Xanthomonas albilineans

<400> 27

Met Asp Ser Ala Leu Pro Thr Ser Ala Phe Thr Phe Asp Leu Phe Tyr
1 5 10 15

Thr Thr Val Asn Ala Tyr Tyr Arg Thr Ala Ala Val Lys Ala Ala Ile
20 25 30

Glu Leu Gly Leu Phe Asp Val Val Gly Gln Gln Gly Arg Thr Pro Ala
35 40 45

Ala Ile Ala Glu Ala Cys Gln Ala Ser Pro Arg Gly Ile Arg Ile Leu
50 55 60

Cys Tyr Tyr Leu Val Ser Ile Gly Phe Leu Arg Arg Asn Gly Gly Leu
65 70 75 80

Phe Tyr Ile Asp Arg Asn Met Ala Met Tyr Leu Asp Arg Ser Ser Pro
85 90 95

Gly Tyr Leu Gly Gly Ser Ile Lys Phe Leu Leu Ser Pro Tyr Ile Met
100 105 110

Ser Ala Phe Thr Asp Leu Thr Ala Val Val Arg Thr Gly Lys Ile Asn
115 120 125

Leu Ala Gln Asp Gly Val Val Ala Pro Asp His Pro Gln Trp Val Glu

```
    130                 135                 140

Phe Ala Arg Ala Met Ala Pro Met Met Ala Leu Pro Ser Ala Leu Ile
145                 150                 155                 160

Ala Asn Met Val Ser Leu Pro Ala Asp Arg Pro Ile Arg Val Leu Asp
                165                 170                 175

Val Ala Ala Gly His Gly Leu Phe Gly Ile Ala Phe Ala Gln Arg Phe
            180                 185                 190

Arg Gln Ala Glu Val Ser Phe Leu Asp Trp Asp Asn Val Leu Asp Val
        195                 200                 205

Ala Arg Glu Asn Ala Gln Ala Ala Lys Val Ala Glu Arg Ala Arg Phe
    210                 215                 220

Leu Pro Gly Asn Ala Phe Asp Leu Asp Tyr Gly Ser Gly Tyr Asp Val
225                 230                 235                 240

Ile Leu Leu Thr Asn Phe Leu His His Phe Asp Glu Val Asp Gly Glu
                245                 250                 255

Arg Ile Leu Ala Lys Thr Arg Asp Ala Leu Asn Asp Asp Gly Met Val
            260                 265                 270

Ile Thr Phe Glu Phe Ile Ala Asp Glu Glu Arg Ser Ser Pro Pro Leu
        275                 280                 285

Ala Ala Thr Phe Ser Met Met Met Leu Gly Thr Thr Pro Ala Gly Glu
    290                 295                 300
```

Ser Tyr Thr Tyr Ser Asp Leu Glu Arg Met Phe Arg His Ala Gly Phe
305 310 315 320

Gly His Val Glu Leu Lys Ser Ile Pro Pro Ala Leu Leu Lys Val Val
325 330 335

Val Ser Arg Lys Arg Ala Pro
340

<210> 28
<211> 167
<212> PRT
<213> Xanthomonas albilineans

<400> 28

Met Ile Glu Ser Ala Thr Ser Pro Val Ala Lys Thr Glu Arg Ile Trp
1 5 10 15

Cys Thr Glu Leu Asp Leu Asp Ala Leu Asn Ala Met Ser Ala Asn Thr
20 25 30

Met Gln Ala Leu Leu Gly Ile Arg Met Ile Glu Ile Gly Ser Asp Tyr
35 40 45

Leu Val Ser Cys Met Ser Val Asp Trp Arg Cys His Gln Pro Tyr Gly
50 55 60

Val Leu His Gly Gly Ala Ser Val Thr Leu Ala Glu Ala Thr Gly Ser
65 70 75 80

Met Ala Ala Ser Met Cys Val Pro Ala Gly Gln Arg Cys Val Gly Leu

85 90 95

Asp Ile Asn Ala Asn His Ile Ala Ser Ile Ser Ser Gly Gln Val Gln
100 105 110

Cys Ile Ala Arg Pro Leu His Ile Gly Ala Leu Thr Gln Val Trp Gln
115 120 125

Met Arg Ile Tyr Asp Glu Gly Asp Arg Thr Ile Cys Val Ser Arg Leu
130 135 140

Thr Met Ala Val Leu Ser Val His Val Ala Arg Val Ser Pro Asn Pro
145 150 155 160

Ala Ser Ser Gly Val Gln Thr
165

<210> 29
<211> 941
<212> PRT
<213> Xanthomonas albilineans

<400> 29

Met Asn Glu Thr Ala Thr Val Thr Lys Ala Thr Leu Ser Ser Ala Lys
1 5 10 15

Ala Ser Ile Thr Pro Ala Cys Val His Gln Trp Phe Glu Ala Gln Val
20 25 30

Ser Ser Thr Pro Asp Ala Pro Ala Ala Phe Leu Gly Glu Arg Arg Met
35 40 45

Ser Tyr Gly Gln Leu Asn Thr Arg Ala Asn Arg Leu Ala Arg Leu Leu
50 55 60

Gln Ser Gln Gly Val Gly Pro Gly Ala Arg Val Ala Val Trp Met Asn
65 70 75 80

Arg Ser Pro Glu Cys Leu Ala Ala Leu Leu Ala Val Met Lys Ala Gly
85 90 95

Ala Ala Tyr Val Pro Ile Asp Leu Ser Leu Pro Ile Arg Arg Val Gln
100 105 110

Tyr Ile Leu Gln Asp Ser Gln Ala Arg Leu Val Leu Val Asp Asp Glu
115 120 125

Gly Gln Gly Arg Leu Asp Glu Leu Glu Leu Gly Ala Met Thr Ala Val
130 135 140

Asp Val Cys Gly Thr Leu Asp Gly Asp Glu Ala Asn Leu Asp Leu Pro
145 150 155 160

Cys Asp Pro Ala Gln Pro Val Tyr Cys Ile Tyr Thr Ser Gly Ser Thr
165 170 175

Gly Ser Pro Lys Gly Val Leu Val Arg His Ser Gly Leu Ala Asn Tyr
180 185 190

Val Ala Trp Ala Lys Arg Gln Tyr Val Thr Ala Asp Thr Thr Ser Phe
195 200 205

Ala Phe Tyr Ser Ser Leu Ser Phe Asp Leu Thr Val Thr Ser Ile Tyr

```
     210                 215                 220

Val Pro Leu Val Ala Gly Leu Cys Val His Val Tyr Pro Glu Gln Gly
225                 230                 235                 240

Asp Asp Val Pro Val Ile Asn Arg Val Leu Asp Asp Asn Gln Val Asp
                245                 250                 255

Val Ile Lys Leu Thr Pro Ser His Met Leu Met Leu Arg Asn Ala Ala
            260                 265                 270

Leu Ala Thr Ser Arg Leu Lys Thr Leu Ile Val Gly Gly Glu Asp Leu
        275                 280                 285

Lys Ala Ala Val Ala Tyr Asp Ile His Gln Arg Phe Arg Arg Asp Val
    290                 295                 300

Ala Ile Tyr Asn Glu Tyr Gly Pro Thr Glu Thr Val Val Gly Cys Ala
305                 310                 315                 320

Ile His Arg Tyr Asp Pro Ala Thr Glu Arg Glu Gly Ser Val Pro Ile
                325                 330                 335

Gly Val Pro Ile Asp His Thr Ser Leu His Leu Leu Asp Glu Arg Leu
            340                 345                 350

Gln Pro Val Ala Pro Gly Glu Val Gly Gln Ile His Ile Gly Gly Ala
        355                 360                 365

Gly Val Ala Ile Gly Tyr Val Asn Lys Pro Glu Ile Thr Asp Ala Gln
    370                 375                 380
```

```
Phe Ile Asp Asn Pro Phe Glu Gly Ser Gly Arg Leu Tyr Ala Ser Gly
385                 390                 395                 400

Asp Leu Gly Arg Met Arg Ala Asp Gly Lys Leu Glu Phe Leu Gly Arg
                405                 410                 415

Lys Asp Ser Gln Ile Lys Leu Arg Gly Tyr Arg Ile Glu Leu Gly Glu
            420                 425                 430

Ile Glu Asn Val Leu Leu Gly His Ala Ala Leu Arg Glu Cys Ile Val
        435                 440                 445

Asp Thr Thr Val Ala Pro Arg Arg Asp Tyr Asp Ser Lys Ser Leu Arg
    450                 455                 460

Tyr Cys Ala Arg Cys Gly Ile Ala Ser Asn Phe Pro Asn Thr Ser Phe
465                 470                 475                 480

Asp Glu His Gly Val Cys Asn His Cys His Ala Tyr Asp Lys Tyr Arg
                485                 490                 495

Asn Val Val Glu Asp Tyr Phe Arg Thr Glu Asp Glu Leu Arg Thr Ile
            500                 505                 510

Phe Glu Gln Val Lys Ala His Asn Arg Leu Arg Tyr Asp Cys Leu Val
        515                 520                 525

Ala Phe Ser Gly Gly Lys Asp Ser Thr Tyr Ala Leu Cys Arg Val Val
    530                 535                 540
```

```
Asp Met Gly Leu Arg Val Leu Ala Tyr Thr Leu Asp Asn Gly Tyr Ile
545                 550                 555                 560

Ser Asp Glu Ala Lys Ala Asn Val Asp Arg Val Val Arg Glu Leu Gly
                565                 570                 575

Val Asp His Arg Tyr Leu Gly Thr Pro His Met Asn Ala Ile Phe Val
            580                 585                 590

Asp Ser Leu His Arg His Ser Asn Val Cys Asn Gly Cys Phe Lys Thr
        595                 600                 605

Ile Tyr Thr Leu Gly Ile Asn Leu Ala His Glu Val Gly Val Ser Asp
    610                 615                 620

Ile Val Met Gly Leu Ser Lys Gly Gln Leu Phe Glu Thr Arg Leu Ser
625                 630                 635                 640

Glu Leu Phe Arg Ala Ser Thr Phe Asp Asn Gln Val Phe Glu Lys Asn
                645                 650                 655

Leu Met Glu Ala Arg Lys Ile Tyr His Arg Ile Asp Asp Ala Ala Ala
            660                 665                 670

Arg Leu Leu Asp Thr Ser Cys Val Arg Asn Asp Arg Leu Leu Glu Ser
        675                 680                 685

Thr Arg Phe Ile Asp Phe Tyr Arg Tyr Cys Ser Val Ser Arg Lys Asp
    690                 695                 700

Met Tyr Arg Tyr Ile Ala Glu Arg Val Gly Trp Ser Arg Pro Ala Asp
```

```
705                 710                 715                 720

Thr Gly Arg Ser Thr Asn Cys Leu Leu Asn Asp Val Gly Ile Tyr Met
                725                 730                 735

His Lys Lys Gln Arg Gly Tyr His Asn Tyr Ser Leu Pro Tyr Ser Trp
            740                 745                 750

Asp Val Arg Val Gly His Ile Pro Arg Glu Asp Ala Met Arg Glu Leu
        755                 760                 765

Glu Asp Thr Asp Asp Ile Asp Glu Ala Lys Val Leu Gly Leu Leu Lys
    770                 775                 780

Gln Ile Gly Tyr Asp Ser Ser Leu Ile Asp Thr Gln Ala Gly Asp Ala
785                 790                 795                 800

Gln Leu Ile Ala Tyr Tyr Val Ala Ala Glu Glu Leu Asp Pro Val Ala
                805                 810                 815

Leu Arg Asn Phe Ala Ala Ala Ile Leu Pro Glu Tyr Met Leu Pro Ser
            820                 825                 830

Tyr Phe Val Arg Leu Asp Arg Met Pro Leu Thr Pro Asn Gly Lys Val
        835                 840                 845

Asn Arg Arg Ala Leu Pro Arg Pro Glu Leu Lys Lys Asn Ala Ser Glu
    850                 855                 860

Ala His Thr Glu Pro Ser Ser Ala Leu Glu Gln Glu Leu Val Gln Ile
865                 870                 875                 880
```

```
Trp Lys Glu Val Leu Met Val Asp Lys Val Gly Val Arg Asp Asn Phe
                885                 890                 895

Phe Glu Leu Gly Gly His Ser Leu Ser Ala Leu Met Leu Leu Tyr Ser
            900                 905                 910

Ile Ala Glu Arg Tyr Gln Lys Met Val Ser Ile Gln Ala Phe Ser Val
        915                 920                 925

Asn Pro Thr Ile Glu Gly Leu Ser Glu His Leu Val Ala
    930                 935                 940
```

<210> 30
<211> 239
<212> PRT
<213> Xanthomonas albilineans

<400> 30

```
Met Asp Leu Gln Cys Ala Arg Ile Ala Ala Leu Cys Glu Gln Leu Lys
1               5                   10                  15

Leu Ala Arg Leu Ser Ser Asp Trp Gln Ala Leu Ala Gln Ala Ala Ala
            20                  25                  30

Cys Glu Asp Ala Ser Tyr Phe Leu Glu Lys Val Leu Ala Ser Glu Gln
        35                  40                  45

Leu Ala Arg Glu Glu Arg Lys Arg Thr Val Leu Thr Arg Leu Ala Arg
    50                  55                  60

Met Pro Ser Ile Lys Thr Leu Glu Gln Phe Asp Trp Ala Gln Ala Gly
```

65 70 75 80

Gly Ala Ser Lys Ala Gln Ile Val Glu Leu Gly His Leu Thr Phe Val
85 90 95

Glu Arg Ala Glu Asn Val Val Met Leu Gly Pro Ser Gly Val Gly Lys
100 105 110

Thr His Ile Ala Leu Ala Leu Cys Gln Arg Ala Val Met Ala Gly His
115 120 125

Lys Ala Arg Phe Ile Thr Ala Ala Asp Leu Met Met Gln Leu Ala Ala
130 135 140

Val Lys Ala Gln Asn Arg Leu Lys Asp Tyr Phe Asn Arg Ala Val Leu
145 150 155 160

Gly Pro Lys Leu Leu Val Val Asp Glu Ile Gly Tyr Leu Pro Phe Gly
165 170 175

Arg Glu Pro Ala Gln Gly Cys Trp Ala Ala Thr Gly Phe Ala Leu Arg
180 185 190

Ser Leu Ala Ala Arg Arg Trp Lys Thr Pro Gly Gly Ser Asp Leu Leu
195 200 205

Arg Arg Phe Lys Gly Lys Trp Val Lys Phe Lys Ser Ala Leu Thr Ala
210 215 220

Asp Val Val Tyr Leu Ile Phe Arg Leu Arg Gly Ser Asp His Pro
225 230 235

<210> 31
<211> 286
<212> PRT
<213> Xanthomonas albilineans

<400> 31

Met Pro Arg Ile Glu Tyr Cys Ile Ser Met Met His Arg Arg Lys Pro
1 5 10 15

Thr Thr Asn Arg Ser Val Cys Met Arg Asp Ile Glu Arg Thr Ala Leu
20 25 30

Trp Val Ala Gly Met Arg Ala Leu Glu Ser Glu Arg Glu Gln Ala Leu
35 40 45

Phe His Asp Pro Phe Ala Arg Arg Leu Ala Gly Asp Glu Phe Val Glu
50 55 60

Glu Leu Arg Arg Asn Asn Gln Asn Val Pro Met Pro Pro Ala Ile Glu
65 70 75 80

Val Arg Thr Arg Trp Leu Asp Asp Lys Ile Met Gln Ala Val Ser Glu
85 90 95

Gly Ile Gly Gln Val Val Ile Leu Ala Ala Gly Met Asp Ala Arg Ala
100 105 110

Tyr Arg Leu Pro Trp Pro Ser Asp Thr Arg Val Tyr Glu Ile Asp His
115 120 125

Met Asp Val Leu Ser Asp Lys His Glu Lys Leu His Asp Ala Gln Pro

130 135 140

Val Cys Gln Arg Ile Ala Leu Pro Ile Asp Leu Arg Glu Asp Trp Pro
145 150 155 160

Gln Ala Leu Lys Glu Ser Gly Phe Val Gly Ser Ala Ala Thr Leu Trp
165 170 175

Leu Val Glu Gly Leu Leu Cys Tyr Leu Ser Ala Glu Ala Val Met Leu
180 185 190

Leu Phe Ala Arg Ile Asp Ala Leu Ser Ala Lys Gly Ser Ser Val Leu
195 200 205

Phe Asp Val Ile Gly Leu Ser Met Leu Asn Ser Pro Asn Ala Arg Val
210 215 220

Leu His Ala Met Ala Arg Gln Phe Gly Thr Asp Glu Pro Glu Ser Leu
225 230 235 240

Ile Gln Pro Leu Gly Trp Glu Pro Gly Val Leu Thr Ile Ala Ala Ala
245 250 255

Gly Gln Gln Met Gly Arg Trp Pro Phe Pro Val Ala Pro Arg Gly Thr
260 265 270

His Gly Val Pro Gln Ser Tyr Leu Val His Ala Leu Lys Arg
275 280 285

<210> 32
<211> 765

<212> PRT
<213> Xanthomonas albilineans

<400> 32

Met Arg Arg Ser Pro Tyr Pro Arg Thr Leu Met Asp Ser Pro Leu Thr
1 5 10 15

Asn Leu Pro Met His Ser Gly Thr Glu Leu Asp Leu Arg Trp Ser Val
20 25 30

Gly Gln Thr Arg Pro Gly Arg Asn Glu Ala Tyr Ala Arg Gln Trp Thr
35 40 45

Thr Leu Leu His Gln Trp Arg Arg Asp Tyr Pro Gly Leu Arg Ile Asp
50 55 60

Val Ser Asp Thr Pro Ile Gly Gln His Ile Thr Ile Asp Tyr Ala Ala
65 70 75 80

Pro Tyr Pro Cys Gly Ser Phe Gly Ser Leu Leu Arg Glu Tyr Ala Arg
85 90 95

Leu Gly Lys Leu Ala Gly Leu Ile Cys Asp Tyr Leu Lys His Arg His
100 105 110

Gln Ile Val Leu Ser Glu Ser Pro Pro Gly Ala Asn Thr Leu Ala Leu
115 120 125

Asp Leu Gly Arg Ile Glu Glu Pro Lys Gln Leu Asp Arg Leu Gln Gly
130 135 140

```
Ala Leu Gly Met Ala Leu Glu Ala Leu Ala Thr Arg Arg Ser Asp Gly
145                 150                 155                 160

Leu Leu Leu Trp His Ala Asp His Arg Gln Arg Asn Leu Pro Asp Leu
                165                 170                 175

Arg Asp Ser Ala Val Cys Gly Ser Ala Ala Gln Ile Ser Leu Pro Ala
            180                 185                 190

Leu Ser Cys Val Glu Asp Leu Ile Glu Val Asp Thr Ser Leu Leu Ala
        195                 200                 205

Cys Asp His Gly Lys Leu Cys Gln Ile Ala Ser His Leu Pro Ala Ser
    210                 215                 220

Trp Phe Ala Arg Ser Thr Asp Gly Pro Met Pro Ser Trp Ser Asp Ala
225                 230                 235                 240

Ser Thr Ala Val Phe Ala Cys Ala Pro Ile Gly Phe Leu Pro Ser Val
                245                 250                 255

Gln Val Asn Val Cys Ala Gln Ile Phe Ser Ala Ala His Leu Ala Ser
            260                 265                 270

Thr Ala Gln Met Ile Asp Pro Leu Arg Gln Gln Ala Phe Ser Tyr Arg
        275                 280                 285

Gln Leu Arg Ser Arg Ala Ala Thr Tyr Ala Arg His Leu Ser Leu Leu
    290                 295                 300

Gly Leu Gln Ser Gly Asp Ala Val Ala Leu Ile Ala Ile Asp Ser Leu
```

305 310 315 320

Ala Gly Val Ala Leu Met Leu Ala Cys Leu Ala Gly Gly Leu Val Phe
325 330 335

Ala Pro Ile Asn Glu Leu Val Ser Leu Val His Phe Glu Thr Thr Leu
340 345 350

Lys Thr Ile Lys Pro Arg Leu Val Leu Ile Asp Ala Glu Leu Pro Pro
355 360 365

Ser His His Ala Ala Leu Arg His Leu Pro Thr Leu Glu Leu Thr Ser
370 375 380

Leu Met Pro Val Ile Glu Asn Asp Glu Leu Val Val Ala Pro Cys Ser
385 390 395 400

Ala Asp Ala Pro Ala Val Met Ile Cys Thr Ser Gly Ser Thr Gly Thr
405 410 415

Pro Lys Ala Val Thr His Ser His Ala Asp Phe Met His Cys His Leu
420 425 430

Asn Tyr Gln Gln Ala Val Leu Gly Leu Arg Ser Asp Asp Val Met Tyr
435 440 445

Thr Pro Ser Arg Leu Phe Phe Ala Tyr Gly Leu Asn Asn Leu Met Leu
450 455 460

Ser Leu Leu Ala Gly Val Ser His Val Ile Ala Ala Pro Leu Ser Val
465 470 475 480

```
Arg Gln Ile Ala Gln Thr Ile His Thr Tyr His Val Thr Val Leu Leu
                485                 490                 495

Ala Val Pro Ala Val Phe Lys Leu Leu Leu Ala Glu Ala Ala Pro Asp
            500                 505                 510

Ala Val Trp Pro Ala Leu Arg Leu Cys Ile Ser Ala Gly Glu Ser Leu
        515                 520                 525

Pro Ala Arg Leu Gly His Ala Ile Ser Thr Arg Trp Gln Val Glu Val
    530                 535                 540

Leu Asp Gly Ile Gly Cys Thr Glu Val Leu Ser Thr Phe Ile Ser Asn
545                 550                 555                 560

Arg Pro Gly His Ala Leu Met Gly Cys Thr Gly Thr Pro Val Pro Gly
                565                 570                 575

Phe Val Val Lys Leu Val Asn Lys Gln Gly Glu Ile Cys Arg Ile Gly
            580                 585                 590

Glu Val Gly Ser Leu Trp Val Arg Gly Asn Thr Leu Thr Arg Gly Tyr
        595                 600                 605

Val Gly Asp Pro Ile Leu Ser Ala Gln Leu Phe Val Asp Gly Trp Phe
    610                 615                 620

Asp Thr Arg Asp Leu Phe Phe Ala Asp Ala Lys Gly Arg Phe His Asn
625                 630                 635                 640
```

```
Leu Gly Arg Met Gly Ser Ala Ile Lys Ile Asn Gly Cys Trp Leu Ser
                645                 650                 655

Pro Glu Thr Leu Glu Ser Val Ile Gln Thr His Ala Cys Val Lys Glu
            660                 665                 670

Cys Ala Ile Cys Leu Ile Glu Asp Glu Phe Gly Leu Pro Arg Pro Ala
        675                 680                 685

Ala Phe Val Val Pro Val Asp Ala Ser Ile Asp Thr Gly Ala Leu Trp
    690                 695                 700

Ala Ala Leu Arg Ala Leu Cys Lys Asn Ala Leu Gly Lys His His Tyr
705                 710                 715                 720

Pro His Leu Phe Val Glu Val Ser Thr Ile Pro Arg Thr Cys Ser Gly
                725                 730                 735

Lys Val Ile Arg Pro Ala Leu Leu Glu Thr Leu Ala Ser Ala Lys His
            740                 745                 750

Leu Gln Ser His Leu Phe Phe Val Gly His Ala Arg Thr
        755                 760                 765
```

<210> 33
<211> 330
<212> PRT
<213> Xanthomonas albilineans

<400> 33

```
Met His Thr Asn Ala Asp Leu Pro Leu Thr Ile Lys Ala Asp Ser Ala
1               5                   10                  15
```

```
Glu Ala Thr Leu Thr Asp Trp Asn Ala Thr His Arg Ala Thr Trp Pro
            20                  25                  30

Thr Leu Leu Trp Gln His Arg Ala Leu Leu Phe Arg Gly Phe Ala His
        35                  40                  45

Pro Gly Gly Leu Glu Gln Ile Ser Arg Cys Phe Phe Asp Glu Arg Leu
    50                  55                  60

Ala Tyr Thr Tyr Arg Ser Thr Pro Arg Thr Asp Val Gly Gln His Val
65                  70                  75                  80

Tyr Thr Ala Thr Glu Tyr Pro Arg Gln Leu Ser Ile Ala Gln His Cys
                85                  90                  95

Glu Asn Ala Tyr Gln Arg Val Trp Pro Met Lys Leu Leu Phe His Cys
            100                 105                 110

Val Gln Pro Ala Ser Glu Gly Gly Cys Thr Pro Leu Ala Asp Met Leu
        115                 120                 125

Lys Val Thr Ala Ala Ile Asp Pro Gln Val Arg Glu Ile Phe Ala Arg
    130                 135                 140

Lys Gln Val Arg Tyr Val Arg Asn Tyr Arg Ala Gly Val Asp Leu Pro
145                 150                 155                 160

Trp Glu Asp Val Phe Asn Thr Arg Asn Lys Gln Glu Val Glu Ala Tyr
                165                 170                 175
```

```
Cys Ala Arg Asn Asp Met Gln Cys Glu Trp Thr Gly Asp Gly Leu Arg
            180                 185                 190

Thr Ser Gln Ile Cys Arg Ala Phe Ala Cys His Pro Ala Thr Gly Asp
        195                 200                 205

Glu Val Trp Phe Asn Gln Ala His Leu Phe His Tyr Thr Ala Leu Glu
    210                 215                 220

Ala Ala Ala Gln Lys Met Met Leu Ser Phe Phe Gly Glu Gln Gly Leu
225                 230                 235                 240

Pro Arg Asn Ala Tyr Phe Gly Asp Gly Thr Pro Ile Asp Pro Ala Met
                245                 250                 255

Leu Asp His Val Arg Thr Val Phe Ala Gln His Lys Ile His Phe Asp
            260                 265                 270

Trp His Arg Asp Asp Val Leu Leu Ile Asp Asn Met Leu Val Ser His
        275                 280                 285

Gly Arg Glu Pro Tyr Glu Gly Ser Arg Lys Ile Leu Val Cys Met Ala
    290                 295                 300

Glu Pro Tyr Ser Pro Glu Gln Ser Ser Pro Asp Ile Ala Ala Arg Ser
305                 310                 315                 320

Asp Gly Glu Ala Met Leu Lys Leu His Val
                325                 330
```

<210> 34

<211> 1959
<212> PRT
<213> Xanthomonas albilineans

<400> 34

Met Lys Leu Ser Ser Met Ser Leu Leu Asp Ala Glu Asp Val Ala Leu
1 5 10 15

Thr Ala Ala Ser Pro Asp Thr Ala Leu Ala Leu Asp Trp Ser Arg Ser
20 25 30

Val Leu Asp Leu Phe Asp Ala Gln Val Ala Leu His Ala Glu Glu Leu
35 40 45

Ala Cys Ala Asp Gln His Arg Gln Leu Ser Tyr Ala Gln Leu Asp Gln
50 55 60

His Ala Asn Arg Leu Ala His Cys Leu Ile Glu Arg Gly Leu Arg Pro
65 70 75 80

Gln Glu Arg Val Ala Leu Trp Phe Gly Arg Ser Pro Asp Phe Leu Ile
85 90 95

Ala Leu Leu Gly Val Leu Lys Ala Gly Gly Cys Tyr Val Pro Leu Asp
100 105 110

Pro His Tyr Pro Thr Thr Tyr Ile Gln Gln Ile Leu Asp Asp Ala Gln
115 120 125

Pro Arg Leu Leu Leu Cys Gly Lys Asp Ile Asp Gly Gln Leu Ile Gln
130 135 140

Val Pro Arg Leu Arg Leu Asp Asp Ala Ala Ile Ala Arg Gln Pro His
145 150 155 160

Thr Pro Leu Pro His Ala Leu His Pro Ala Gln Leu Ala Tyr Val Met
165 170 175

Tyr Thr Ser Gly Ser Thr Gly Arg Pro Lys Gly Val Met Val Pro His
180 185 190

Arg Gln Ile Leu Asn Trp Leu His Ala Leu Trp Ala Arg Ala Pro Phe
195 200 205

Glu Ala Gly Glu Arg Val Ala Gln Lys Thr Ser Ile Ala Phe Ala Ile
210 215 220

Ser Val Lys Glu Leu Leu Ala Gly Leu Leu Ala Gly Val Pro Gln Val
225 230 235 240

Phe Ile Asp Glu Asp Thr Val Arg Asp Ile Pro Ala Phe Val Arg Ala
245 250 255

Leu Glu Thr Trp Gln Ile Thr Arg Leu Tyr Thr Phe Pro Ser Gln Leu
260 265 270

Asn Ala Leu Leu Asp His Val Ala Glu Thr Pro Gln Arg Leu Ala Arg
275 280 285

Leu Arg Gln Leu Phe Val Ser Ile Glu Pro Cys Pro Ala Glu Leu Leu
290 295 300

Gln Arg Leu Arg Thr Leu Leu Pro Ala Cys Thr Ala Trp Tyr Ile Tyr

305 310 315 320

Gly Cys Thr Glu Ile Asn Asp Met Thr Tyr Cys Asp Pro Ala Glu Gln
325 330 335

His Ser Gly Ser Gly Phe Val Pro Val Gly Arg Pro Ile Ala Asn Thr
340 345 350

Lys Val His Val Leu Asp Glu Gln Leu Arg Pro Leu Pro Pro Gly Ile
355 360 365

Met Gly Glu Val His Ile Glu Ser Leu Gly Ile Thr His Gly Tyr Trp
370 375 380

Arg Gln Gly Gly Leu Thr Ala Ala Arg Phe Ile Ala Asn Pro Tyr Gly
385 390 395 400

Pro Pro Gly Ser Arg Leu Tyr Arg Thr Gly Asp Met Ala Arg Leu Leu
405 410 415

Asp Asn Gly Thr Leu Glu Leu Leu Gly Arg Arg Asp Tyr Glu Val Lys
420 425 430

Val Arg Gly Tyr Arg Val Asp Val Arg Gln Val Glu Lys Ala Leu Ala
435 440 445

Ala His Leu Gln Val Ala Glu Ala Ala Val Ile Gly Trp Pro Gln Gly
450 455 460

Ser Pro Thr Pro Glu Leu Leu Ala Tyr Val Val Pro Arg Gln Gly Val
465 470 475 480

```
Leu Asn Leu Asp Glu Leu Arg Lys Leu Leu Gln Glu Arg Leu Pro Thr
                485                 490                 495

Tyr Met Leu Pro Thr Arg Phe Gln Ser Leu Pro Ala Leu Pro Arg Leu
            500                 505                 510

Pro Asn Gly Lys Leu Asp Thr Leu Ser Leu Pro Glu Pro Gln Ala Ala
        515                 520                 525

Ser Ser Asp Ser Asp Tyr Leu Ala Pro Arg Ser Glu Val Glu Ile Thr
    530                 535                 540

Leu Ala Lys Leu Trp Ser Glu Leu Leu Thr Pro Ala Gln Ala Ala Pro
545                 550                 555                 560

Leu Arg Val Ser Leu Asn Asp Asn Phe Phe Asn Leu Gly Gly His Ser
                565                 570                 575

Leu Leu Ala Thr Gln Leu Phe Ser Arg Ile Arg Gln Ser Phe Asp Ile
            580                 585                 590

Glu Val Arg Val Asn Thr Leu Phe Glu Ser Pro Val Leu Glu Asp Phe
        595                 600                 605

Ala Arg Val Val Asn Glu Ala Arg Gln Gln Gln Ala Pro Thr Gly Gly
    610                 615                 620

Asn Thr Ile Ser Ser Arg Ala Val Arg Asp Ala Pro Val Pro Leu Ser
625                 630                 635                 640
```

```
Tyr Gln Gln Glu Arg Leu Trp Phe Val His Glu His Met Pro Glu Gln
                645                 650                 655

Arg Thr Ser Tyr Asn Val Ala Phe Ala Cys His Leu Arg Ser Ala Asp
            660                 665                 670

Phe Ser Met Ser Ala Leu Arg Glu Ala Ile Gln Ala Leu Val Ala Arg
        675                 680                 685

His Glu Thr Leu Arg Thr Arg Ile Ala Thr Cys Ala Gly Gly Asp Tyr
    690                 695                 700

Pro Ser Gln His Ile Ala Asp Ala Met Gln Val Pro Val Pro Cys Ile
705                 710                 715                 720

Thr Ala Thr Pro Ala Glu Val Pro Arg Leu Val Ala Glu His Ala Ala
                725                 730                 735

His Val Phe Asp Leu Ala His Gly Pro Leu Leu Lys Val Ser Val Leu
            740                 745                 750

Arg Val Ser Asp Asp Tyr His Val Phe Leu Met Asn Met His His Ile
        755                 760                 765

Ile Cys Asp Gly Trp Ser Ile Asn Leu Ile Phe His Asp Leu Arg Ala
    770                 775                 780

Phe Tyr Ile Ala Ala Leu Gln Gln Thr Pro Pro Ala Leu Pro Pro Leu
785                 790                 795                 800

Leu Leu Gln Tyr Ala Asp Tyr Ala Thr Trp Gln Arg Val Gln Asp Phe
```

805 810 815

Ser Ala Asp Leu Asp Tyr Trp Lys Gln Arg Leu His Gly Tyr Glu Glu
820 825 830

Gly Leu Ala Leu Pro Tyr Asp Phe Pro Arg Pro Ala Asn Arg Ala Trp
835 840 845

Arg Ala Gly Ile Leu His Leu Thr Tyr Pro Asp Ala Leu Ala Ala Arg
850 855 860

Leu Ala Ala Phe Ser Gln Glu Arg Arg Val Thr Leu Phe Met Thr Leu
865 870 875 880

Met Ala Ser Leu Ala Ile Val Leu His Gln Tyr Thr Gly Arg Arg Glu
885 890 895

Leu Cys Leu Gly Thr Thr Ser Ala Gly Arg Asp Gln Leu Glu Thr Glu
900 905 910

Asn Leu Ile Gly Phe Phe Val Asn Ile Leu Ala Val Arg Leu Asn Leu
915 920 925

Gly Ser His Ala Phe Ala Glu Asp Phe Leu Gln His Val Arg Gln Gln
930 935 940

Val Leu Asp Ala Tyr Ala His Arg Ala Leu Pro Phe Glu His Val Leu
945 950 955 960

Ser Ala Leu Lys Lys Pro Arg Asp Ser Ser Gln Ile Pro Leu Val Pro
965 970 975

Ile Met Leu Arg His Gln Asn Phe Ala Thr Glu Gly Val Asn Ala Phe
980 985 990

Ala Gln Ile Phe Leu Ser Ala Gln Met Glu Phe Gly Glu Arg Thr Thr
995 1000 1005

Pro Asn Glu Leu Asp Leu Gln Phe Ile Gly Asp Gly Ser His Leu
1010 1015 1020

Glu Val Thr Val Glu Tyr Ala Ala Glu Leu Phe Ser Ala Ala Thr
1025 1030 1035

Val Gln Arg Met Leu Ala His His Gln Arg Val Leu Glu Arg Met
1040 1045 1050

Leu Glu Glu Pro Arg Cys Arg Leu Ser Asp Phe Ser Leu Pro Val
1055 1060 1065

Ala Arg Thr Glu Phe Thr Pro His Thr Leu Asp Thr Ser Arg Ser
1070 1075 1080

Val Leu Asp Leu Phe Asp Ala Gln Val Ala Leu His Ala Glu Glu
1085 1090 1095

Leu Ala Cys Ala Asp Gln His Arg Gln Leu Ser Tyr Ala Gln Leu
1100 1105 1110

Asp Gln His Ala Asn Arg Leu Ala His Cys Leu Ile Glu Arg Gly
1115 1120 1125

Leu Arg Pro Gln Glu Arg Val Ala Leu Trp Phe Gly Arg Ser Pro
1130 1135 1140

Asp Phe Leu Ile Ala Leu Leu Gly Val Leu Lys Ala Gly Gly Cys
1145 1150 1155

Tyr Val Pro Leu Asp Pro His Tyr Pro Thr Thr Tyr Ile Gln Gln
1160 1165 1170

Ile Leu Asp Asp Ala Gln Pro Arg Leu Leu Leu Cys Gly Lys Asp
1175 1180 1185

Ile Asp Gly Gln Leu Ile Gln Val Pro Arg Leu Arg Leu Asp Asp
1190 1195 1200

Ala Ala Ile Ala Arg Gln Pro His Thr Pro Leu Pro His Ala Leu
1205 1210 1215

His Pro Ala Gln Leu Ala Tyr Val Met Tyr Thr Ser Gly Ser Thr
1220 1225 1230

Gly Arg Pro Lys Gly Val Met Val Pro His Arg Gln Ile Leu Asn
1235 1240 1245

Trp Leu His Ala Leu Trp Ala Arg Ala Pro Phe Glu Ala Gly Lys
1250 1255 1260

Arg Val Ala Gln Lys Thr Ser Ile Ala Phe Ala Ile Ser Val Lys
1265 1270 1275

Glu Leu Leu Ala Gly Leu Leu Ala Gly Val Pro Gln Val Phe Ile

1280 1285 1290

Asp Glu Asp Thr Val Arg Asp Ile Pro Ala Phe Val Arg Ala Leu
1295 1300 1305

Glu Thr Trp Gln Ile Thr Arg Leu Tyr Thr Phe Pro Ser Gln Leu
1310 1315 1320

Asn Ala Leu Leu Asp His Val Ala Glu Thr Pro Gln Arg Leu Ala
1325 1330 1335

Arg Leu Arg Gln Leu Phe Val Ser Ile Glu Pro Cys Pro Ala Glu
1340 1345 1350

Leu Leu Gln Arg Leu Arg Thr Leu Leu Pro Ala Cys Thr Ala Trp
1355 1360 1365

Tyr Ile Tyr Gly Cys Thr Glu Ile Asn Asp Met Thr Tyr Cys Asp
1370 1375 1380

Pro Ala Glu Gln His Ser Gly Ser Gly Phe Val Pro Val Gly Arg
1385 1390 1395

Pro Ile Ala Asn Thr Lys Val His Val Leu Asp Glu Gln Leu Arg
1400 1405 1410

Pro Leu Pro Pro Gly Ile Met Gly Glu Val His Ile Glu Ser Leu
1415 1420 1425

Gly Ile Thr His Gly Tyr Trp Arg Gln Gly Gly Leu Thr Ala Ala
1430 1435 1440

Arg Phe Ile Ala Asn Pro Tyr Gly Pro Pro Gly Ser Arg Leu Tyr
1445 1450 1455

Arg Thr Gly Asp Met Ala Arg Leu Leu Asp Asn Gly Thr Leu Glu
1460 1465 1470

Leu Leu Gly Arg Arg Asp Tyr Glu Val Lys Val Arg Gly Tyr Arg
1475 1480 1485

Val Asp Val Arg Gln Val Glu Lys Ala Leu Ala Ala His Leu Gln
1490 1495 1500

Val Ala Glu Ala Ala Val Ile Gly Trp Pro Gln Gly Ser Pro Thr
1505 1510 1515

Pro Glu Leu Leu Ala Tyr Val Val Pro Arg Gln Gly Val Leu Asn
1520 1525 1530

Leu Asp Glu Leu Arg Lys Leu Leu Gln Glu Arg Leu Pro Thr Tyr
1535 1540 1545

Met Leu Pro Thr Arg Phe Gln Ser Leu Pro Ala Leu Pro Arg Leu
1550 1555 1560

Pro Asn Gly Lys Leu Asp Thr Leu Ser Leu Pro Glu Pro Gln Ala
1565 1570 1575

Ala Ser Ser Asp Ser Asp Tyr Leu Ala Pro Arg Ser Glu Val Glu
1580 1585 1590

Ile Thr Leu Ala Lys Leu Trp Ser Glu Leu Leu Thr Pro Ala Gln
1595 1600 1605

Ala Ala Pro Leu Arg Val Ser Leu Asn Asp Asn Phe Phe Asn Leu
1610 1615 1620

Gly Gly His Ser Leu Leu Ala Thr Gln Leu Phe Ser Arg Ile Arg
1625 1630 1635

Gln Ser Phe Asp Ile Glu Val Arg Val Asn Thr Leu Phe Glu Ser
1640 1645 1650

Pro Val Leu Glu Asp Phe Ala Ala Val Val Glu Arg Gly Met Arg
1655 1660 1665

Gln Ser Gln Ala Gly Ser Met Pro Val Ser Leu Ile Val Pro Leu
1670 1675 1680

Ser Leu Arg Thr Glu Arg Ala Ala Val Tyr Ala Ile His Pro Ile
1685 1690 1695

Gly Gly Gln Ile His Cys Tyr Ile Asp Leu Ala Ala Ala Leu Gly
1700 1705 1710

His Ser Ala Arg Val Tyr Gly Leu Gln Cys Glu Pro Val Arg Arg
1715 1720 1725

Phe Ala His Leu Ser Asp Leu Ala Ala His Tyr Cys Asp Ala Leu
1730 1735 1740

Leu Ala Gly Pro Thr Gly Ala Pro Tyr Arg Leu Leu Gly Trp Ser

1745 1750 1755

Ser Gly Gly Val Leu Ala Leu Ala Val Ala Glu Gln Leu Gln Arg
1760 1765 1770

Arg Gly Leu Arg Val Asp Tyr Val Gly Leu Leu Asp Ser Ser Leu
1775 1780 1785

Ile Pro Val His Ala Arg Glu Pro Arg Gln Leu Thr Phe Val Ala
1790 1795 1800

Ala Leu Asn Thr Leu Ala Ala Leu Ala Lys Arg Gly Phe Glu Gln
1805 1810 1815

Ala Glu Ile Asp Glu Ala Arg Gln Leu Leu Phe Ala Asp Gly Asp
1820 1825 1830

Asp Glu His Val Phe Asp Tyr Ser Arg His Gln Ala Ser Leu Asp
1835 1840 1845

Lys Leu Leu Ala His Leu Arg Phe Thr Leu Glu Ser Arg Met Trp
1850 1855 1860

Pro Pro Leu Ala Glu Gln Leu Arg Val Thr Arg Tyr His Leu Gly
1865 1870 1875

Leu Leu Ala Gly Phe Glu Pro Gln Cys Leu Gln Pro Asn Ala His
1880 1885 1890

Leu Tyr Gln Ala Gln Thr Ala Val His Val Ser Tyr Ala Asp Met
1895 1900 1905

Ser Lys Pro Arg Gly Gly Ser Glu Val Leu Pro Asp Ile Thr Gly
1910 1915 1920

Tyr Val Pro Leu Ser Gln Ile Lys Ser Ala Ala Gly Asn His Tyr
1925 1930 1935

Ser Met Leu Gln Gly Asp Pro Leu Arg Glu Leu Ala Arg Met Leu
1940 1945 1950

Val Thr Asp Leu Asp Ala
1955

<210> 35
<211> 83
<212> PRT
<213> Xanthomonas albilineans

<400> 35

Met Thr Phe Glu Glu Gln Ala Tyr Leu Val Leu Ile Asn Asp Glu Leu
1 5 10 15

Gln Tyr Ser Leu Trp Pro Ser Asp Leu Glu Val Pro Pro Gly Trp Arg
20 25 30

Lys Glu Gly Tyr Ala Gly Gly Lys Asp Glu Cys Met Ala Tyr Ile Asp
35 40 45

Glu Thr Trp Thr Asp Met Arg Pro Leu Ser Leu Arg Glu Leu Asp Asp
50 55 60

Lys Asn Leu Gly Asp Ala Ser Ser Pro Asp Gly Ser Gly Phe Glu Ser

65 70 75 80

Ser Tyr Ser

<210> 36
<211> 315
<212> PRT
<213> Xanthomonas albilineans

<400> 36

Met Gly Cys Ala Cys Leu Pro His Tyr Leu Glu Lys Gln Asp Leu Ser
1 5 10 15

Ala Leu Asp Asp Ala Leu Ala Gly Val Arg Leu Ser Gln Tyr Cys Thr
20 25 30

Thr Asp Gly Arg Gln Leu Glu Leu Tyr Trp Leu Gly Ala Gln Ala Ser
35 40 45

Pro Lys Leu Val Leu Leu Pro Pro Tyr Gly Met Ser Tyr Leu Leu Leu
50 55 60

Ser Arg Leu Ala Gln Arg Leu Ala Arg His Phe His Val Leu Cys Trp
65 70 75 80

Glu Ser Ile Gly Cys Pro Asn Ala Gln Thr Ser Val Thr Ala Glu Asp
85 90 95

Phe Asp Leu Asp Arg Gln Ala Ala Thr Leu Leu Gly Ile Leu His Gln
100 105 110

His Asp Tyr Ala Asp Cys His Phe Val Gly Trp Cys Gln Ala Ala Gln
115 120 125

Leu Ala Val His Ala Ile Ala Leu His Gly Phe Ala Pro Arg Ser Met
130 135 140

Ala Trp Val Ala Pro Ala Gly Leu Leu Pro Pro Ile Val Lys Ser Glu
145 150 155 160

Phe Glu Arg Cys Ala Leu Pro Ile Tyr Leu Gln Ile Glu Arg His Gly
165 170 175

Leu Glu Gln Ala Lys Lys Leu Ala Ala Ile Leu Asp Lys Tyr Arg Gly
180 185 190

Gln Pro Leu Arg Gly Asp Asp Leu Ala Glu Lys Leu Thr Met Leu His
195 200 205

Leu Ala Asp Pro Ala Ser Thr Leu Val Phe Ser Arg Tyr Met Arg Ala
210 215 220

Tyr Glu Glu Asn Lys Gln Ser Val Gln Ala Leu Leu Pro Thr Ala Leu
225 230 235 240

Gly Arg His Pro Thr Leu Ile Val His Cys Lys Asp Asp Ser Phe Ser
245 250 255

His Tyr Ser Ala Ser Val Gln Leu Ala Arg His Asp Pro Ser Leu Arg
260 265 270

Leu Asp Leu Leu Asp His Gly Gly His Leu Gln Leu Phe Asn Asp Pro

275 280 285

Gly Ala Val Ala Gln Arg Ile Ile Asp Phe Ile Gly Leu Thr Val Gly
290 295 300

Glu Val Ala Pro Thr Ser Met His Ser Ala Ala
305 310 315

<210> 37
<211> 451
<212> PRT
<213> Xanthomonas albilineans

<400> 37

Met Tyr Ile Pro Asn Asn Ile Asp Leu Asp Pro His Ser Ala Leu Val
1 5 10 15

Arg Gln Leu Thr Ser Tyr Gln Val Arg Phe Leu Gln Trp Trp Arg Leu
20 25 30

Arg Gly Pro Ser Glu Phe His Asp Arg Glu Met Asn Leu Arg Met Pro
35 40 45

Thr Gly Gly Val Lys Gly Ser Glu Trp Thr Arg Tyr His Arg Met Arg
50 55 60

Pro Ser Asp Tyr Arg Trp Gly Val Phe Met Met Pro Pro Asp Arg Asn
65 70 75 80

Thr Val Val Phe Gly Glu Arg Lys Gly Gln Val Ala Trp Ser Cys Val
85 90 95

```
Pro Glu Glu Tyr Arg Asp Leu Leu Leu Asp His Val Thr Val Gln Gly
          100                 105                 110

Asp Val Glu Asn Ala Ala Val Glu Gln Ser His Glu Leu Thr Gln Met
        115                 120                 125

Val Pro Ser Ala Ile Asp Leu Glu His Leu Phe Gln Phe Phe Leu Glu
    130                 135                 140

Glu Gly Arg His Thr Trp Ala Met Ser His Leu Leu Ile Glu Tyr Phe
145                 150                 155                 160

Gly Ser Asp Gly Ala Asp Ala Ala Glu Gly Leu Leu Gln Arg Met Ser
                165                 170                 175

Gly Asp Ala Gln Asn Pro Arg Leu Leu Asp Ala Phe Asn Tyr His Thr
            180                 185                 190

Glu Asp Trp Leu Ser His Phe Met Trp Cys Phe Phe Ala Asp Arg Val
        195                 200                 205

Gly Lys Tyr Gln Ile Gln Ala Val Thr Gln Ser Ala Phe Leu Pro Leu
    210                 215                 220

Ala Arg Thr Ala Arg Phe Met Met Phe Glu Glu Pro Leu His Ile Lys
225                 230                 235                 240

Phe Gly Val Asp Gly Leu Glu Arg Val Leu Tyr Arg Ser Ala Glu Ile
                245                 250                 255

Thr Leu Arg Glu Asp Thr His Ala Ile Phe Asp Ala Gly Ala Ile Pro
```

260 265 270

Leu Pro Val Val Gln Lys Tyr Leu Asn Tyr Trp Leu Pro Lys Ile Phe
275 280 285

Asp Leu Phe Gly His Asp Val Ser Glu Arg Ser Arg Val Leu Tyr Gln
290 295 300

Ala Gly Ile Arg Ser Pro Arg Asn Phe Asp Lys Leu Glu Gly Thr Glu
305 310 315 320

Val Ala Val Asp Val Arg Cys Glu Asp Arg Leu Val Ser Ser Thr Ala
325 330 335

Pro Ala Glu Leu Ala Ile Asn Ala Val Met Arg Arg Gln Tyr Ile Ala
340 345 350

Glu Val Gly Ala Ile Ile Gly Arg Trp Asn Gln Gln Leu Arg Arg Leu
355 360 365

Gly Leu Ala Phe Glu Leu Gln Leu Pro His Glu Arg Phe His Arg Asp
370 375 380

Phe Gly Pro Cys Lys Gly Leu Ala Phe Asp Leu Asp Gly Asn Pro Val
385 390 395 400

His Asp Ala Asp Gly Gln Arg Leu Ala Ala Leu Leu Pro Thr Pro Gln
405 410 415

Asp Leu Ala Gly Val Arg Gly Leu Met Gly Arg Glu Leu Gly Glu Gly
420 425 430

Arg Thr Ala Val Trp Leu Ala Pro Ala Gly Ala Ser Leu Asp Lys Leu
435 440 445

Met Pro Ala
450

<210> 38
<211> 317
<212> PRT
<213> Xanthomonas albilineans

<400> 38

Met Asn Ser Tyr Val Gly Cys Gln Lys Leu Glu Thr Asp Gly Asp Ala
1 5 10 15

Ser Arg Val Val Pro Met Trp Val Met Tyr Pro Thr Ala Thr Pro Ser
20 25 30

Arg Asp Thr Ala Met Gly Pro Tyr Thr Leu Asp Val Ala Leu Gly Ala
35 40 45

Pro Ile Glu Ala Gly Pro Phe Pro Leu Ala Val Ile Ser His Gly Thr
50 55 60

Arg Ser Ala Gly Leu Val Phe Arg Thr Leu Ala His Tyr Leu Ala Arg
65 70 75 80

His Gly Phe Ile Val Ala Leu Pro Glu His Pro Gly Asp Asn Leu Phe
85 90 95

Gln His Gln Leu Glu Tyr Ser Tyr Gln Asn Leu Glu Asp Arg Pro Arg

100 105 110

His Ile Arg Ala Val Ile Asp Thr Leu Thr Gly His Ala Gln Phe Gly
115 120 125

Pro Ala Ile Gln Ala His Asn Val Ala Val Ile Gly His Ser Val Gly
130 135 140

Gly Tyr Thr Ala Leu Ala Ile Ala Gly Gly Glu Pro His Thr Gly Phe
145 150 155 160

Met Val Asp Phe Ala His Arg Pro Glu His Ala Glu Gln Pro Ala Trp
165 170 175

Thr Ala Leu Val Arg Gln Asn Arg Val Pro Ile Arg Ala Val Pro Val
180 185 190

Thr Ala Asp Pro Arg Val Arg Ala Val Val Ala Leu Ala Pro Asp Phe
195 200 205

Ser Leu Tyr Met His Glu Asp Ala Leu Ala Lys Val Glu Val Pro Val
210 215 220

Leu Leu Ile Val Gly Glu Lys Asp Gln Trp Ala His Glu Thr Ile Val
225 230 235 240

Ala Thr Arg Thr Ala Leu Gly Asn Asp Gly Arg Leu Glu Ala Arg Val
245 250 255

Val Pro Asn Ala Gly His Tyr Ala Phe Ile Ser Val Phe Pro Glu Ala
260 265 270

Met Lys Ala Arg Val Gly Glu Ala Ala Ile Asp Pro Pro Gly Phe Asp
275 280 285

Arg Ser Ala Phe Gln Arg Glu Leu Glu Arg Asp Ile Leu His Phe Leu
290 295 300

Thr Val Thr Met Arg Pro Ala Glu Ala Ala Ile Ser Gly
305 310 315

<210> 39
<211> 496
<212> PRT
<213> Xanthomonas albilineans

<400> 39

Met Gln Lys Pro Lys Glu Ala Leu Gly Met Pro Pro Gly Met Ala Pro
1 5 10 15

Pro Gly Ala Gln Phe Asp Tyr Arg Trp Arg Trp Pro Ala Met Ile Val
20 25 30

Leu Leu Ser Ala Asn Phe Met Asn Leu Leu Asp Val Gly Ile Val Asn
35 40 45

Val Ala Leu Pro Ser Ile Gln Lys Asn Leu Gly Ala Asp Glu Gln Gln
50 55 60

Leu Glu Trp Ile Val Ala Ile Tyr Ile Leu Leu Phe Ala Leu Gly Leu
65 70 75 80

Leu Pro Leu Gly Arg Leu Gly Asp Met Leu Gly Arg Lys Arg Met Phe

85 90 95

Gly Thr Gly Val Ala Gly Phe Ile Leu Met Ser Ala Phe Cys Ala Ile
100 105 110

Ala Gly Asn Ile His Val Leu Ile Ile Ala Arg Ala Leu Gln Gly Leu
115 120 125

Ala Ala Ala Met Leu Ala Pro Gln Val Met Ala Ile Ala Gln Thr Met
130 135 140

Phe Ala Pro Lys Glu Arg Ala Ala Ala Phe Ser Leu Phe Gly Leu Val
145 150 155 160

Ala Gly Leu Ala Ser Phe Ala Gly Pro Leu Val Ser Gly Leu Leu Ile
165 170 175

His Ile Asp Ala Phe Gly Val Gly Trp Arg Ala Ile Phe Leu Ile Asn
180 185 190

Val Pro Ile Gly Leu Val Thr Leu Leu Ala Ala Ala Ile Trp Val Pro
195 200 205

Lys Val Pro Ala His Ala Gly Ile His Asn Asp Trp Val Gly Ile Ala
210 215 220

Leu Ala Ala Leu Ala Leu Leu Cys Leu Val Phe Pro Leu Ile Glu Gly
225 230 235 240

Arg Ala Tyr Gly Trp Pro Leu Trp Cys Phe Ala Ala Ile Ala Leu Gly
245 250 255

Ile Pro Leu Leu Val Ala Phe Val Ala Trp Gln Arg Arg Gln Ala His
260 265 270

Leu Ala Arg Pro Ala Leu Leu Pro Ile Tyr Leu Met Ser His Arg Asp
275 280 285

Tyr Ile Leu Gly Ala Leu Ser Val Ser Val Phe Tyr Ser Ala Leu Gln
290 295 300

Gly Phe Phe Leu Val Phe Val Ile Phe Leu Gln Gln Gly Leu Ala Tyr
305 310 315 320

Ser Ala Leu Glu Thr Gly Val Ala Thr Thr Pro Phe Pro Val Gly Val
325 330 335

Ala Ile Ala Ser Met Leu Ala Arg His Val Glu Ser Leu Arg Ala Lys
340 345 350

Ile Phe Ser Gly Ala Cys Leu Met Ile Ala Ser Tyr Leu Ala Leu Trp
355 360 365

Val Ile Ile Thr Arg Ser Glu Gly Ser Leu Asp Pro Trp Thr Leu Thr
370 375 380

Leu Pro Leu Leu Ile Gly Gly Leu Gly Cys Gly Ile Thr Ile Ala Ser
385 390 395 400

Leu Phe Gln Thr Val Met Arg Thr Val Pro Leu Lys Asp Ala Gly Ala
405 410 415

Gly Ser Gly Ala Leu Gln Val Ile Gln Gln Val Gly Gly Met Leu Gly
420 425 430

Ile Ala Leu Val Ser Glu Ile Phe Phe Ser Gly Leu His Gln His Leu
435 440 445

Gln Gly Pro Ala Gly Val Ala Leu Ala Phe Lys Gln Ala Phe Gly Ala
450 455 460

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20 25 30

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35 40 45

Phe Gln Arg Ala Ile Lys Leu Val His Glu Tyr Gly Asp Pro Gly Ala
50 55 60

Glu Leu Val Val Ala Thr Ser Trp Ser Gly Gln Thr Pro Glu Leu Met
65 70 75 80

Arg Glu Gly Leu Gly Lys Thr Ala Gln Ala Val Asp Gln Tyr Arg Ser
85 90 95

Ala Phe Gly Asp Leu Pro Trp His Val Asn Lys Gln Phe Val Ala Gln
100 105 110

Ser Phe Phe Tyr Arg Ser Gln Leu Ala Met Val Glu His Pro Gly His
115 120 125

Leu Leu Glu Tyr Asp Leu Ser His Met Ala Glu Pro Ala Phe Lys Pro
130 135 140

Pro Ser Tyr Arg His Tyr Glu His His Leu Thr His Ala Val Ala Gly
145 150 155 160

Cys Tyr Thr Ser Pro Phe Glu Glu Ala Val Cys Ala Val Leu Asp Gly
165 170 175

Met Gly Glu Lys Asn Ala Leu Ala Cys Tyr His Tyr Gln Gln Gly Lys
180 185 190

Leu Thr Pro Ile His Gln Ser Glu Thr Ser Ser Trp Ala Ser Leu Gly
195 200 205

Phe Phe Tyr Gly Met Ile Cys Glu Val Cys Gly Phe Gly Thr Leu Ser
210 215 220

Gly Glu Glu Trp Lys Val Met Gly Leu Ala Ala Tyr Gly Gln His Asp
225 230 235 240

Arg Gln Leu Tyr Glu Leu Leu Arg Gln Met Leu Arg Val Asp Gly Leu
245 250 255

Thr Leu Arg Phe Ala Pro Ala Ala Gln Phe Ser Gln Leu Gln Arg Thr
260 265 270

Leu Tyr Ala Met Arg Arg Cys Lys Gly Gln Pro Thr Ile Glu Leu Ala
275 280 285

Asn Leu Ala Tyr Ala Gly Gln Gln Val Phe Cys Asp Val Leu Phe Glu
290 295 300

Phe Leu His Asn Leu His Ala Leu Gly Leu Ser Asp His Leu Val Leu
305 310 315 320

Gly Gly Gly Cys Ala Leu Asn Ser Ser Ala Asn Gly Arg Val Leu Ala
325 330 335

Glu Thr Pro Phe Arg His Leu His Val Phe Ala Ala Pro Gly Asp Asp
340 345 350

Gly Asn Ala Val Gly Ala Ala Leu Trp Ala His Ala Glu Asp His Pro
355 360 365

Glu Gln Thr Pro Pro Ala Ala Arg Glu Gln Ser Pro Tyr Leu Gly Ser
370 375 380

Ser Met Ser Ala Glu Thr Leu His Asn Val Glu Arg Phe Gly Ala Leu

385 390 395 400

Ser Lys Phe Thr Arg Cys Leu Asp Asp Ala Ala Gln Arg Ala Ala Arg
405 410 415

Leu Leu Thr Glu Gly Lys Ile Val Ala Trp Val Gln Gly Arg Ala Glu
420 425 430

Phe Gly Pro Arg Ala Leu Gly Asn Arg Ser Ile Leu Ala Asp Pro Arg
435 440 445

Ser Pro Ala Ile Lys Asp Ile Ile Asn Ala Arg Val Lys Phe Arg Glu
450 455 460

Glu Phe Arg Pro Phe Ala Pro Ser Ile Leu His Glu His Gly Ala Glu
465 470 475 480

Tyr Phe Glu Leu Tyr Gln Glu Ser Pro Tyr Met Glu Arg Thr Leu Lys
485 490 495

Phe Arg Ala Glu Ala Thr Arg Lys Val Pro Gly Val Val His His Asp
500 505 510

Gly Thr Gly Arg Leu Gln Thr Val Lys Gln His Trp Asn Pro Arg Tyr
515 520 525

His Ala Leu Ile Lys Glu Phe Tyr Arg Leu Thr Gly Ile Pro Leu Val
530 535 540

Leu Asn Thr Ser Phe Asn Val Met Gly Lys Pro Ile Ala His Ser Val
545 550 555 560

Glu Asp Ala Leu Ser Ile Phe Phe Thr Ser Gly Leu Asp Ala Met Phe
565 570 575

Ile Asp Asp Val Leu Ile Glu Lys
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<400> 41

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1 5 10 15

Gln Ala Asp Ala Gly Val Pro Val Lys Asp Ile Cys Arg Gln Val Gly
20 25 30

Ile Ser Thr Ala Thr Tyr Tyr Gln Trp Lys Ser Lys Tyr Val Ala Ser
35 40 45

Glu Met Pro Ser Ser Arg His Thr Ser Leu Thr Trp Arg Pro Pro Ser
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Thr Cys Phe Ser Val Ala Thr Ile Trp Leu Ser Val Asn Leu Leu Leu
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Arg Ile Val Gly Arg Leu Gly Gly
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<400> 42

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1 5 10 15

Ala Asp Tyr Val Ala Gln Ile Phe Gly Glu Asp Pro Leu Val Val His
20 25 30

Asn Asp Glu Tyr Ser Trp His Glu Leu Lys Asp Arg Gly Gly Phe Ser
35 40 45

Ser Ile Ile Val Ser Pro Gly Pro Gly Ser Val Val Asn Glu Ala Asp
50 55 60

Phe His Ile Ser Leu Gln Ala Leu Glu Gln Asn Glu Phe Pro Val Leu
65 70 75 80

Gly Val Cys Leu Gly Phe Gln Gly Leu Ala His Val Tyr Gly Gly Arg
85 90 95

Ile Leu His Ala Pro Val Pro Phe His Gly Arg Arg Ser Thr Val Ile
100 105 110

Asn Thr Gly Asp Gly Leu Phe Glu Gly Ile Pro Gln Arg Phe Glu Ala
115 120 125

Val Arg Tyr His Ser Leu Met Val Cys Gln Gln Ser Leu Pro Pro Val
130 135 140

Leu Lys Val Thr Ala Arg Thr Asp Cys Gly Val Val Met Gly Leu Gln
145 150 155 160

His Val Gln His Pro Lys Trp Gly Val Gln Phe His Pro Glu Ser Ile
165 170 175

Leu Thr Glu His Gly Lys Arg Ile Val Ala Asn Phe Ala Lys Leu Ala
180 185 190

Ala Arg His Ser Ala Pro Leu Leu Ala Gly Ser Glu Gln Ala Gly Lys
195 200 205

Val Leu Ser Val Cys Ala Pro Glu Met Val Thr Pro Arg Val Arg Arg
210 215 220

Met Leu Ser Arg Lys Ile Lys Cys Arg Trp Gln Ala Glu Asp Val Phe
225 230 235 240

Leu Ala Leu Phe Ala Asp Glu Lys His Cys Phe Trp Leu Asp Ser Gln
245 250 255

Leu Val Cys Ser Pro Met Ala Arg Tyr Ser Phe Met Gly Ala Val Asn
260 265 270

Glu Ser Glu Val Val Arg His Cys Val Arg Pro Gly Ser Met Val Gln
275 280 285

Glu Ala Gly Glu Arg Phe Leu Ala Glu Met Asp Arg Ala Leu Gln Ser
290 295 300

Val Leu Thr Glu Asp Val Ala Glu Arg Pro Pro Phe Ala Phe Arg Gly

305 310 315 320

Gly Tyr Val Gly Tyr Met Ser Tyr Glu Met Lys Ser Val Phe Gly Ala
325 330 335

Pro Ala Ser His Ala Asn Ala Ile Pro Asp Ala Leu Trp Met Arg Val
340 345 350

Glu Arg Phe Val Ala Phe Asp His Ala Thr Glu Glu Val Trp Leu Leu
355 360 365

Ala Leu Ala Asp Thr Glu Asp Leu Ser Ala Leu Ala Trp Leu Asp Ala
370 375 380

Ile Glu Gln Arg Ile His Ala Ile Gly Gln Ala Ala Pro Ala Cys Ile
385 390 395 400

Ser Leu Gly Leu Arg Ser Met Glu Ile Glu Leu Asn His Gly Arg Arg
405 410 415

Gly Tyr Leu Glu Ala Ile Glu Arg Cys Lys Gln Arg Ile Val Asp Gly
420 425 430

Glu Ser Tyr Glu Ile Cys Leu Thr Asp Leu Phe Ser Phe Gln Ala Glu
435 440 445

Leu Asp Pro Leu Met Leu Tyr Arg Tyr Met Arg Arg Gly Asn Pro Ala
450 455 460

Pro Phe Gly Ala Tyr Leu Arg Asn Gly Ser Asp Cys Ile Leu Ser Thr
465 470 475 480

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Ser Pro Glu Arg Phe Leu Glu Val Asp Gly His Gly Thr Ile Gln Thr
                485                 490                 495

Lys Pro Ile Lys Gly Thr Cys Arg Arg Ala Glu Asp Pro Gln Leu Asp
            500                 505                 510

Arg Asn Leu Ala Met Arg Leu Ala Ala Ser Glu Lys Asp Arg Ala Glu
        515                 520                 525

Asn Leu Met Ile Val Asp Leu Met Arg Asn Asp Leu Ser Arg Val Ala
    530                 535                 540

Val Pro Gly Ser Val Thr Val Pro Lys Leu Met Asp Ile Glu Ser Tyr
545                 550                 555                 560

Lys Thr Val His Gln Met Val Ser Thr Val Glu Ala Arg Leu Arg Ala
                565                 570                 575

Asp Cys Ser Leu Val Asp Leu Leu Lys Ala Val Phe Pro Gly Gly Ser
            580                 585                 590

Ile Thr Gly Ala Pro Lys Leu Arg Ser Met Glu Ile Ile Asp Gly Leu
        595                 600                 605

Glu Asn Ala Pro Arg Gly Val Tyr Cys Gly Ser Ile Gly Tyr Leu Gly
    610                 615                 620

Tyr Asn Cys Val Ala Asp Leu Asn Ile Ala Ile Arg Ser Leu Ser Tyr
625                 630                 635                 640
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Asp Gly Gln Glu Ile Arg Phe Gly Ala Gly Gly Ala Ile Thr Phe Leu
645 650 655

Ser Asp Pro Gln Asp Glu Phe Asp Glu Val Leu Leu Lys Ala Glu Ala
660 665 670

Ile Leu Lys Pro Ile Trp His Tyr Leu His Ala Pro Asn Thr Pro Leu
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<400> 43

Met Arg Pro Pro Arg Leu Arg Ala Asn Gln Asp Gly Leu Leu Met Asp
1 5 10 15

Thr Ala Gly Arg Val Val Glu Gly Cys Thr Ser Asn Leu Phe Leu Val
20 25 30

Glu Asn Gly His Leu Val Thr Pro Asp Leu Gly Val Ala Gly Val Ser
35 40 45

Gly Ile Met Arg Gly Arg Val Ile Glu Tyr Gly Arg Gln His Gly Leu
50 55 60

Ala Cys Ala Val Lys His Val Tyr Pro Asp Gln Leu Val Arg Ala Gln
65 70 75 80

Glu Val Phe Leu Thr Asn Ala Val Phe Gly Ile Leu Leu Val Arg Ser
85 90 95

Ile Asp Ala His Ser Tyr Arg Ile Asp Pro Val Thr Leu Arg Leu Leu
100 105 110

Asp Ala Leu Cys Gln Gly Val Tyr Phe Thr Glu Arg Ser Leu His Gln
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Val Ser Thr His Ala Gly Gln Asp Pro
130 135

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<400> 44

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Val Ser Glu Asp Arg Ser Gly Gln Ser Leu Glu Ser Ile Arg Phe Glu
20 25 30

Asp Cys Thr Phe Arg Gln Cys Asn Phe Thr Glu Ala Glu Leu Asn Arg
35 40 45

Cys Lys Phe Arg Glu Cys Glu Phe Val Asp Cys Asn Leu Ser Leu Ile

50 55 60

Ser Ile Pro Gln Thr Ser Phe Met Glu Val Arg Phe Val Asp Cys Lys
65 70 75 80

Met Leu Gly Val Asn Trp Thr Ser Ala Gln Trp Pro Ser Val Lys Met
85 90 95

Glu Gly Ala Leu Ser Phe Glu Arg Cys Ile Leu Asn Asp Ser Leu Phe
100 105 110

Tyr Gly Leu Tyr Leu Ala Gly Val Lys Met Val Glu Cys Arg Ile His
115 120 125

Asp Ala Asn Phe Thr Glu Ala Asp Cys Glu Asp Ala Asp Phe Thr Gln
130 135 140

Ser Asp Leu Lys Gly Ser Thr Phe His Asn Thr Lys Leu Thr Gly Ala
145 150 155 160

Ser Phe Ile Asp Ala Val Asn Tyr His Ile Asp Ile Phe His Asn Asp
165 170 175

Ile Lys Arg Ala Arg Phe Ser Leu Pro Glu Ala Ala Ser Leu Leu Asn
180 185 190

Ser Leu Asp Ile Glu Leu Ser Asp
195 200

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<212> PRT
<213> Xanthomonas albilineans

<400> 45

Met His Pro Pro Ser Pro Leu Asn Thr Gln Gln Lys Asp Trp Leu Thr
1 5 10 15

Arg Gly Gly Ser Leu Thr Ala His Leu Arg Leu Leu Gly Gln Val Gln
20 25 30

Val Gln Val Gln Arg Glu His Lys Ser Met Ala Trp Leu Asp Glu Tyr
35 40 45

Arg Val Leu Gly Leu Ser Arg Cys Leu Leu Val Trp Val Arg Glu Val
50 55 60

Val Leu Val Val Asp Ala Lys Pro Tyr Val Tyr Ala Arg Ser Leu Thr
65 70 75 80

Pro Leu Thr Ala Ser Tyr Asn Ala Trp Gln Ala Val Arg Ser Ile Gly
85 90 95

Ser Arg Pro Leu Ala Asp Leu Leu Phe Arg Asp Arg Ser Val Leu Arg
100 105 110

Ser Ala Leu Ala Ser Arg Arg Ile Thr Ala Gln His Pro Leu His Arg
115 120 125

Arg Ala Cys Asn Phe Val Ala Gln Ser His Ala Thr Gln Ala Leu Leu
130 135 140

Ala Arg Arg Ser Val Phe Thr Arg Gln Gly Ala Pro Leu Leu Ile Thr
145 150 155 160

Glu Cys Met Leu Pro Ala Leu Trp Ala Thr Leu Glu Pro Val Ala Ala
165 170 175

Pro Arg Gln Ala Ser Leu Ser Ala Asp Gly Pro Cys Arg His Ser Ala
180 185 190

Gln Ile Val Ser Pro Glu Ser Met Leu Glu
195 200

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1 5 10 15

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20 25 30

Gln Pro Leu Gln Leu Ser Leu Ala Pro Glu Leu Gln Ala Ala Ala Arg
35 40 45

Ser Ala His Arg His Leu Leu Asp Asp Gly Thr Ala Leu Tyr Leu Leu
50 55 60

Ala Phe Asp Thr Ala Gln Phe Asp Pro Gly Ala Phe Ala Ala Met Ala
65 70 75 80

Ile Ala Arg Pro Asp Ser Ile Ala Arg Ser Val Arg Lys Arg Gln Ala
85 90 95

Glu Phe Leu Phe Gly Arg Leu Ala Ala Arg Leu Ala Leu Gln Glu Val
100 105 110

Leu Gly Pro Ala Gln Ala Gln Ala Asp Ile Ala Ile Gly Ala Thr Arg
115 120 125

Ala Pro Cys Trp Pro Ala Gly Ser Leu Gly Ser Ile Ser His Cys Glu
130 135 140

Asp Tyr Ala Ala Ala Ile Ala Met Ala Ala Gly Thr Arg His Gly Val
145 150 155 160

Gly Ile Asp Leu Glu Arg Pro Ile Thr Pro Ala Ala Arg Ala Ala Leu
165 170 175

Leu Ser Ile Ala Ile Asp Ala Asp Glu Ala Ala Arg Leu Ala Lys Ala
180 185 190

Ala Asp Ala Gln Trp Pro Gln Asp Leu Leu Leu Thr Ala Leu Phe Ser
195 200 205

Ala Lys Glu Ser Leu Phe Lys Ala Ala Tyr Ser Ala Val Gly Arg Tyr
210 215 220

Phe Asp Phe Ser Ala Ala Arg Leu Cys Gly Ile Asp Leu Ala Arg Gln
225 230 235 240

Cys Leu His Leu Arg Leu Thr Glu Thr Leu Cys Ala Gln Phe Val Ala
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Leu Thr His Tyr Ala Trp
275

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20 25 30

Ile Phe Leu Arg Glu Leu Ile Ser Asn Ala Ser Asp Ala Ala Asp Lys
35 40 45

Leu Arg Phe Glu Ala Leu Val Lys Pro Glu Leu Leu Asp Gly Asp Ala
50 55 60

Gln Leu Arg Ile Arg Ile Gly Phe Asp Lys Asp Ala Gly Thr Val Thr
65 70 75 80

Ile Asp Asp Asn Gly Ile Gly Met Ser Arg Glu Glu Ile Val Ala His
85 90 95

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Leu Gly Thr Ile Ala Lys Ser Gly Thr Ser Asp Phe Leu Lys His Leu
            100                 105                 110

Ser Gly Asp Gln Lys Lys Asp Ser His Leu Ile Gly Gln Phe Gly Val
        115                 120                 125

Gly Phe Tyr Ser Ala Phe Ile Val Ala Asp Gln Val Asp Val Tyr Ser
    130                 135                 140

Arg Arg Ala Gly Leu Pro Ala Ser Asp Gly Val His Trp Ser Ser Arg
145                 150                 155                 160

Gly Glu Gly Glu Phe Glu Val Ala Thr Ile Asp Lys Pro Glu Arg Gly
                165                 170                 175

Thr Arg Ile Val Leu His Leu Lys Glu Glu Glu Lys Gly Phe Ala Asp
            180                 185                 190

Gly Trp Lys Leu Arg Ser Ile Val Arg Lys Tyr Ser Asp His Ile Ala
        195                 200                 205

Leu Pro Ile Glu Leu Ile Lys Glu His Tyr Gly Glu Asp Lys Asp Lys
    210                 215                 220

Pro Glu Thr Pro Glu Trp Glu Thr Val Asn Arg Ala Ser Ala Leu Trp
225                 230                 235                 240

Thr Arg Pro Arg Thr Glu Ile Lys Asp Glu Glu Tyr Gln Glu Leu Tyr
                245                 250                 255
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Lys His Ile Ala His Asp His Glu Asn Pro Val Ala Trp Ser His Asn
           260                 265                 270

Lys Val Glu Gly Lys Leu Glu Tyr Thr Ser Leu Leu Tyr Leu Pro Gly
       275                 280                 285

Arg Ala Pro Phe Asp Leu Tyr Gln Arg Asp Ala Ser Arg Gly Leu Lys
   290                 295                 300

Leu Tyr Val Gln Arg Val Phe Ile Met Asp Gln Ala Asp Gln Phe Leu
305                 310                 315                 320

Pro Leu Tyr Leu Arg Phe Ile Lys Gly Ile Val Asp Ser Ser Asp Leu
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Pro Leu Asn Val Ser Arg Glu Ile Leu Gln Ser Gly Pro Val Ile Asp
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Ser Met Lys Ser Ala Leu Thr Lys Arg Ala Leu Asp Met Leu Glu Lys
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Leu Ala Lys Asp Asp Pro Glu Arg Tyr Lys Gly Val Trp Lys Asn Phe
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Gly Gln Val Leu Lys Glu Gly Pro Ala Gln Asp Phe Gly Asn Arg Glu
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Lys Ile Ala Gly Leu Leu Arg Phe Ala Ser Thr His Ser Gly Asp Asp
                405                 410                 415

Ala Gln Asn Val Ser Leu Ala Asp Tyr Val Ala Arg Met Lys Asp Gly
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420 425 430

Gln Asp Lys Leu Tyr Tyr Leu Thr Gly Glu Ser Tyr Ala Gln Ile Lys
435 440 445

Asp Ser Pro His Leu Glu Val Phe Arg Lys Lys Gly Ile Glu Val Leu
450 455 460

Leu Leu Thr Asp Arg Ile Asp Glu Trp Leu Met Ser Tyr Leu Thr Glu
465 470 475 480

Phe Asp Ser Lys Ser Phe Val Asp Val Ala Arg Gly Asp Leu Asp Leu
485 490 495

Gly Lys Leu Asp Ser Glu Glu Glu Lys Gln Ala Gln Glu Glu Ala Ala
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Lys Ala Lys Gln Gly Leu Ala Glu Arg Ile Gln Gln Val Leu Lys Asp
515 520 525

Glu Val Ala Glu Val Arg Val Ser His Arg Leu Thr Asp Ser Pro Ala
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Ile Leu Ala Ile Gly Gln Gly Asp Met Gly Leu Gln Met Arg Gln Ile
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Leu Glu Ala Ser Gly Gln Lys Leu Pro Glu Ser Lys Pro Val Phe Glu
565 570 575

Phe Asn Pro Ala His Pro Leu Ile Glu Lys Leu Asp Ala Glu Pro Asp
580 585 590

Val Asp Arg Phe Gly Asp Leu Ala Arg Val Leu Phe Asp Gln Ala Ala
595 600 605

Leu Ala Ala Gly Asp Ser Leu Lys Asp Pro Ala Ala Tyr Val Arg Arg
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Leu Asn Lys Leu Leu Leu Glu Leu Ser Ala
625 630

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gctggaaacc gagaatctga 20

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<400> 50
gacacgatca gccgctagga 20

<210> 51

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<400> 51
accagcagtt gggccagcct 20

<210> 52
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<212> DNA
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<400> 52
tgcccacagg ccgtcgagt 19

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<400> 53
gcgagaggac aagctgctgc 20

<210> 54
<211> 20
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<213> Xanthomonas albilineans

<400> 54
cgttgaggat gcagcgctcg 20

CLAIMS:

We claim:

1. DNA molecules encoding the Albicidin Biosynthetic Gene Clusters and proteins selected from the group consisting of:

(a) isolated DNA fragments which encode proteins that in turn individually and collectively perform functions in Albicidin Biosynthesis;

(b) isolated DNA which hybridizes to isolated DNA of (a) above and that encodes a protein that in turn performs an individual function in Albicidin Biosynthesis; and

(c) isolated DNA differing from the isolated DNAs of (a) and (b) above in codon sequence due to the degeneracy of the genetic code, and which encodes a protein that in turn performs as function in Albicidin Biosynthesis

(d) isolated DNA selected from the group of DNA molecules having a sequence that is at least 70% homologous with a DNA comprising one or more of SEQ. ID. Nos.1 to 25.

2. Isolated DNA molecules of claim 1 comprising any one of SEQ ID No.1, SEQ ID No. 2 or SEQ ID No. 3.

3. A vector comprising a purified and isolated DNA molecule(s) of claim 1 operably linked to promoters.

4. A host cell comprising an isolated DNA molecule of claim 1.

5. A host cell comprising the isolated DNA molecule of claim 2.

6. A host cell comprising a vector of claim 3.

7. A method of producing a protein, wherein said protein consists of an amino acid sequence selected from the group consisting of SEQ ID Nos. 26 to 48, comprising the steps of: expressing DNA molecules of Claim 1 in a host cell, wherein said DNA molecules encodes a protein, and wherein the expression of said DNA molecules leads to the production of Albicidins by said cell.

8. A method of producing a polyketide carrying para-aminobenzoic acid and/or carbamoyl benzoic acid by inserting at least one DNA Fragment of Claim 1 that encodes a PKS protein into a cell and causing the cell to express the encoded PKS protein under conditions such that the PKS protein functions to produce a polyketide carrying either a para-aminobenzoic acid or a carbamoyl benzoic acid or both.

9. A method of producing polyketide/peptides carrying para-aminobenzoic acid and/or carbamoyl benzoic acid by inserting at least one DNA Fragment of Claim 1 that encodes a PKS protein into a cell and causing the cell to express the encoded PKS protein under conditions such that the PKS protein functions to produce a polyketide carrying either a para-aminobenzoic acid or a carbamoyl benzoic acid or both.

10. A method of activating nonproteinogenic amino acids like paraminobenzoic acid and/or carbamoyl benzoic acid for incorporation into peptides or polyketides by inserting at least one DNA Fragment of Claim 1 that encodes a PKS protein into a cell and causing the cell to express the encoded PKS protein under conditions such that the PKS protein functions to produce a polyketide carrying either a para-aminobenzoic acid or a carbamoyl benzoic acid or both.

11. Proteins encoded by the DNA of Claim 1.

12. Proteins encoded by the DNA of Claim 2.

13. An isolated and purified antibiotic produced by a process that includes at least three proteins coded by DNA sequences of claim 1 in combination with additional enzymes that modify the product to provide a non-naturally

occurring Albicidin-like product having at least one of the useful properties reported for albicidin.

14. An antibiotic or antibiotics of claim 13 having at least one of the general structures illustrated in Figure 11.

15. An antibiotic produced by the process of expressing the DNA of one or more of the genes included in the Albicidin Biosynthetic Gene Clusters of Claim 1 in a genetically modified host cell sustained in a culture media, and thereafter separating the antibiotic from the host cell and culture media.

16. A process for producing an antibiotic that comprises modifying a host cell to enhance expression of the DNA of claim 1 by insertion of expression enhancing DNA into the genome of a *Xanthomonas albilineans* strain, *Escherichia coli* strain, or other Albicidin producing microbial strain, in a position operative to enhance expression of the enzymes of the Albicidin Biosynthetic Gene Clusters, culturing the modified host cell to produce an antibiotic and isolating the antibiotic.

17. An isolated purified antibiotic having at least 4 of the structural elements illustrated in Figure 11, and an elemental composition of $C_{40}H_{35}N_6O_{15}$.

18. A method of protecting a plant against damage from albicidin that comprises applying an agent that blocks expression at least one gene in the Albicidin Biosynthetic Gene Clusters of claim 1 to the plant to be protected.

19. A method of obtaining agents useful in blocking expression of albicidin by screening materials against a modified host cell line that expresses the Albicidin Biosynthesis Gene Clusters of claim 1 and selecting for materials that stop or decrease albicidin production.

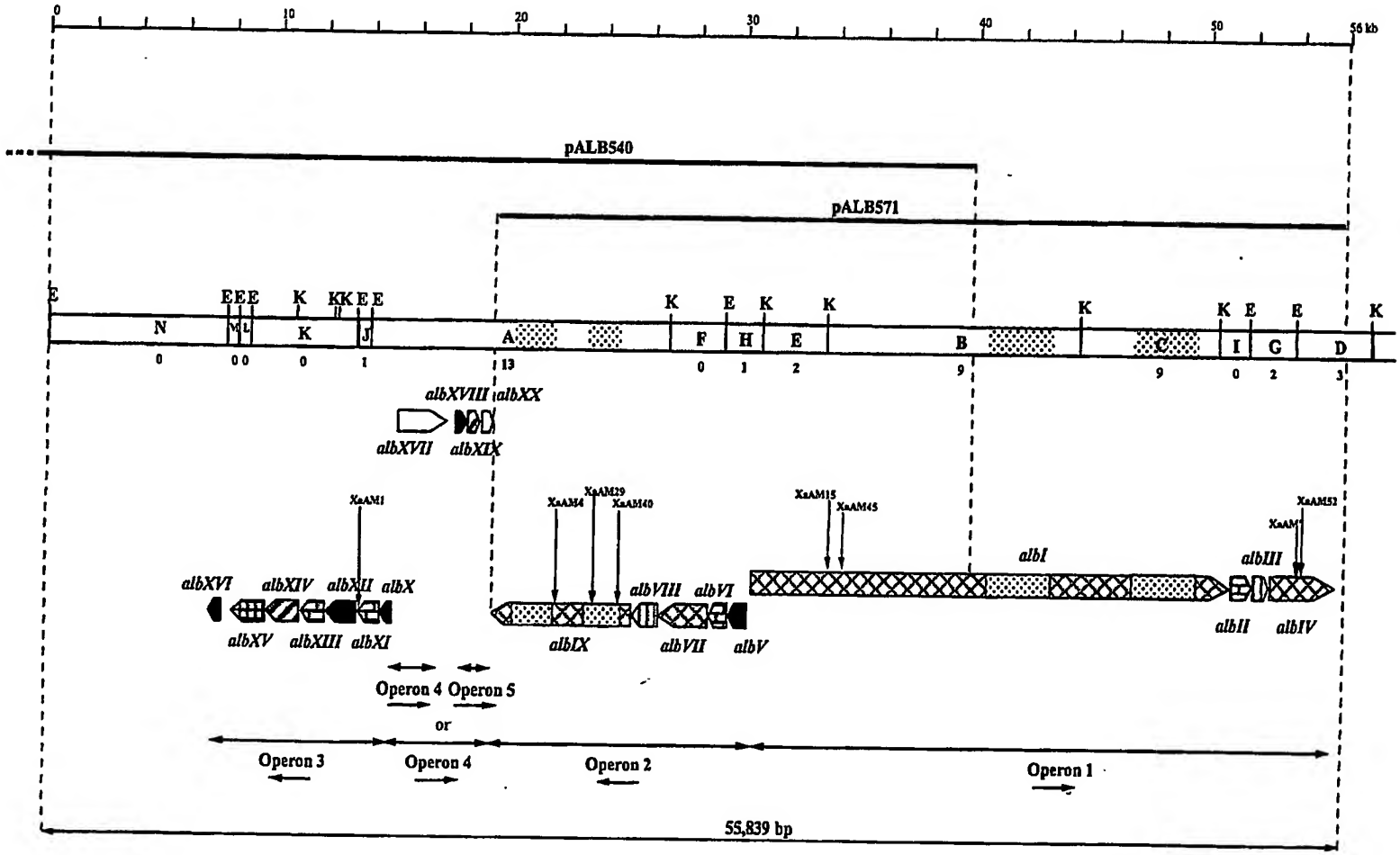
20. A method of protecting a plant against phytotoxic damage from an antibiotic that comprises inserting into the plant and operably expressing at least one

resistance gene from the Albicidin Biosynthesis Gene Clusters of claim 1 in the plant to be protected.

21. A plant reproductive part carrying an albicidin resistance gene of claim 1 selected from the group consisting of seeds, propagative materials and plant parts.

ABSTRACT

Three gene clusters that together encode albicidin biosynthesis, the complete gene DNA sequences, the deduced protein sequences for the enzymes and methods for using the DNA sequences are disclosed and discussed as well as methods for plant protection and creating new antibiotics. The novel Albicidin family of antibiotics is disclosed and their structure deduced.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albXV
albXIII
albXI
albIX
albVII
albV
albVIII
albVI
albI
albIII
albII
albIV
Operon 4
Operon 5
or
Operon 3
Operon 4
Operon 2
Operon 1
55,839 bp

Figure 1

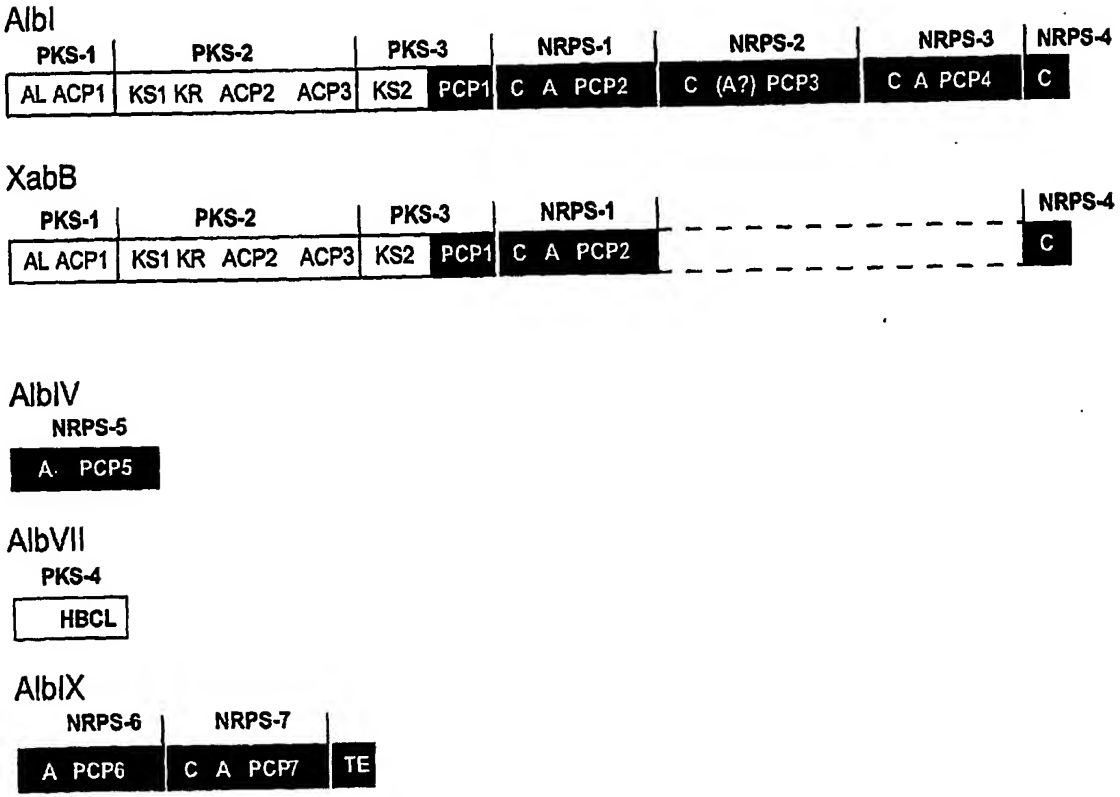

AlbI
PKS-1
PKS-2
PKS-3
NRPS-1
NRPS-2
NRPS-3
NRPS-4
AL ACP1
KS1 KR ACP2 ACP3
KS2
PCP1
C A PCP2
C (A?) PCP3
C A PCP4
C
XabB
PKS-1
PKS-2
PKS-3
NRPS-1
NRPS-4
AL ACP1
KS1 KR ACP2 ACP3
KS2
PCP1
C A PCP2
C
AlbIV
NRPS-5
A PCP5
AlbVII
PKS-4
HBCL
AlbIX
NRPS-6
NRPS-7
A PCP6
C A PCP7
TE

Figure 2

Sgl-TcmO	173	FVDLGGARG	234	PRADVFIV	263	ALTPGGAVLV
Sgl-TcmN	331	IADLGGGDG	393	TGYDAYLF	423	IGDDDARLLI
Smy-MdmC	64	VLEIGTFTG	135	GAFDIVFV	159	LVRPGGLVAI
Mxa-SafC	63	TLEVGVFTG	134	GTFDLAFI	158	LVRPGGLIIL
Ser-EryG	85	VLDVGFGLG	149	ETFDRVTS	178	VLKPGGVLAI
Spe-DauK	183	VLDVGGGKG	254	RKADAIIL	273	ALEPGGRILI
Sal-DmpM	208	VVDIGGADG	269	GGGDLYVL	298	AMPAHARLLV
Shy-RapM	106	VLEVGCGMG	155	VQGDAEEL	194	ALRRGGALSH
Sav-AveD	71	VLDVGCGSG	124	GSFDAAWA	151	VLRPGGRLAV
Sar-Cmet	158	VLDVACGHG	220	GPYDLSLI	251	ATRPGGRIGI
AlbII	174	VLDVAAGHG	236	SGYDVILL	267	ALNDDGMVIT
		Motif I		Motif II		Motif III

Figure 3

Sgl-tcmP	84	VVLHLACGLDSRAFRMDVPD	109	DVDVPDVIELR	139	EDWLDTVP	150	PALVVAEGLTPYL
Sme-PKS	84	TVLHLGCGLDSRIFRIDPGP	109	ELDVPDVISLR	139	RGWIERLP	150	PTMIVAEGVLPYL
Pmu-tcmP	86	VVVQLGAGLDARFERLGKPQ	111	DLDLPEVINIR	141	TDWMKTVS	152	PVLLILEGVLMFF
Mtu-Omt	85	TVVALAEGLQTSFWRLDVAI	113	TVDLPPIVDLR	144	YSWMDSVD	155	GVFITAEGLLMYL
Mlo-Hp	84	IVLHLGCGLDTRVFRVDPPP	109	DADYPQVIELR	139	PGWLAEVP	150	PAMVVAEGLTPYL
Mtu-Hp	101	QVAILASGLDSRAYRLPWPT	127	EIDQPKVMEFK	162	ADWPTALQ	178	PTAWLAEGLLIYL
Mtu-Hp2	104	QVVILASGDLSRAWRLPWPD	129	ELDQPKVLEFK	162	QDWPKALQ	178	PCAWLAEGLVRYL
Mtu-Hp3	98	QVVILAAGLDSRAYRLPWPD	123	ELDRPQVLDFK	156	DDWPQALR	172	PSAWIAEGLLIYL
Mtu-Hp4	101	QAVIVAAGLDCRAYRLDWQP	126	EIDVPKVLEFK	161	TDWPTPLT	177	PSAWSVEGLLPYL
Sco-Hp	93	QVVLLGAGMDSRAFRMAWPE	118	EVDTPAPLEFK	153	EDWPSALA	169	PTAWIGEGLLIYL
AlbVI	99	QVVILAAGMDARAYRLPWPS	124	EIDHMDVLSDK	157	EDWPQALK	173	ATLWLVEGLLCYL
		Motif I		Motif II		Motif III		Motif IV			

Figure 4

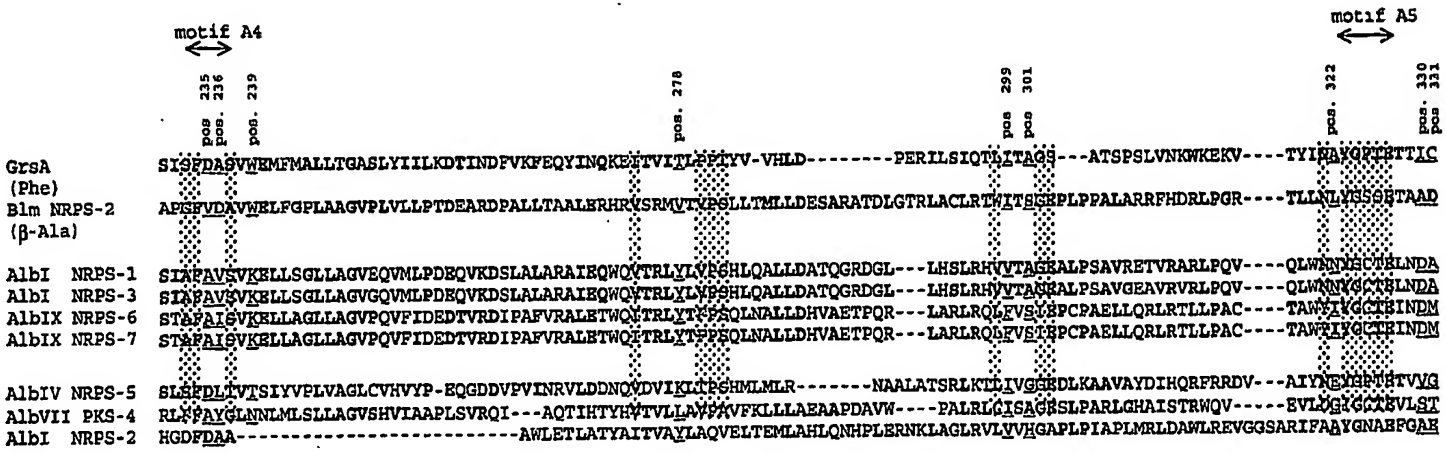

motif A4
motif A5
pos. 235
pos. 236
pos. 239
pos. 278
pos. 299
pos 301
pos. 322
pos. 330
pos 331
GrsA (Phe)
Blm NRPS-2 (β-Ala)
AlbI NRPS-1
AlbI NRPS-3
AlbIX NRPS-6
AlbIX NRPS-7
AlbIV NRPS-5
AlbVII PKS-4
AlbI NRPS-2

Figure 5

XALB1 Strand +
29 bp downstream from the TGA stop codon of *albXVII*

```
            -40  -35  -30  -25  -20  -15  -10   -5  -1+  +5                 p      s
17085=>  ACCATTGTGAACGGCCTTCCCGCTTCGTCCATAGCGATTTTCGATCGCGGC              4.30      0
                                  ----      ----
                                     ---       ---
```

XALB1 Strand +
400 bp downstream from the TAA stop codon of *albIV*

```
            -40  -35  -30  -25  -20  -15  -10   -5  -1+  +5                 p      s
55617=> CATGGCTGCAGGCCGAGCTCGCTCAGCTACGGGGTGAGACCGAAGCTGCCC <= 55667     4.13     12
                     ----      ----
                  -- --      -- --
```

XALB1 Strand –
62 bp, 170 bp and 560 bp downstream from the TAG stop codon of *albXVI*

```
           -40  -35  -30  -25  -20  -15  -10   -5  -1+  +5                 p      s
 7030=> GGGGGGCAGTTGCCCGGACCCCGGTTTCTGTAAACGTTTGGCTGTCTGTAG <= 6879      3.95     13
                              ----      ----
                           -- --      -- --

 6922=> AACTCTTAAAAGAGATTGATTTAAATTTCCCTGCGTTTTTGTACGAGAATA <= 6872      4.42      0

 6532=> TACTTAATATAAGATTGCGAAGCTTGCGTTGCGGAATGATTTTTTCAATAT <= 6482      4.27     53
                           -- --    -- --
                     --- -- ---      --- -- ---
```

XALB3 Strand+

```
            -40  -35  -30  -25  -20  -15  -10   -5  -1+  +5                 p      s
 8065=> GCAAAGAAAAGCGGAAACGAAAAAAGGGCCTACGGGCCCTTTTTTCTTCCA              4.78      0

 8072=> AAAGCGGAAACGAAAAAAGGGCCTACGGGCCCTTTTTTCTTCCATCGTCGA              3.94     86
                     ------------      ------------
                      ----- -- --       -- -- -----
```

Figure 6

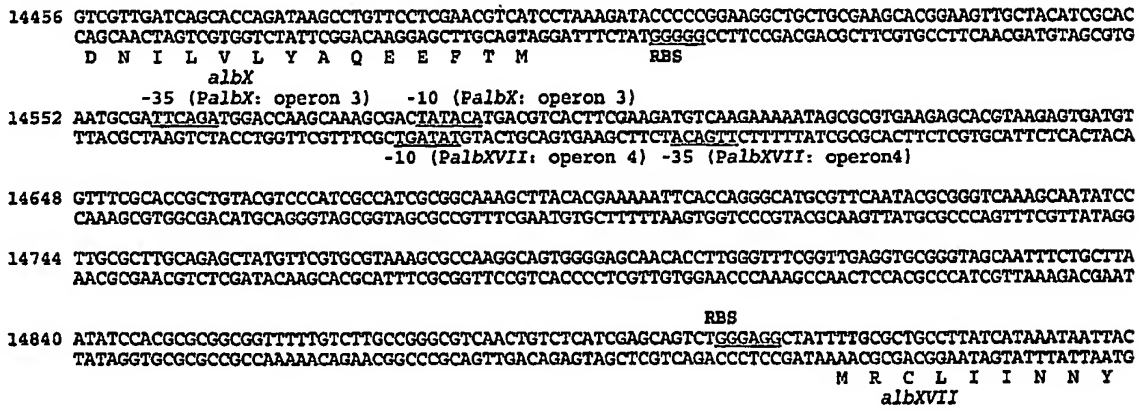


Figure 7A

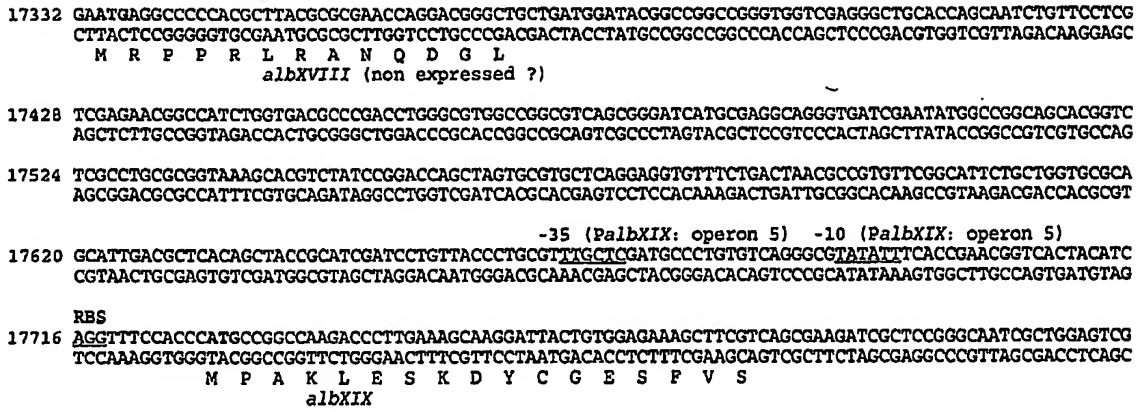
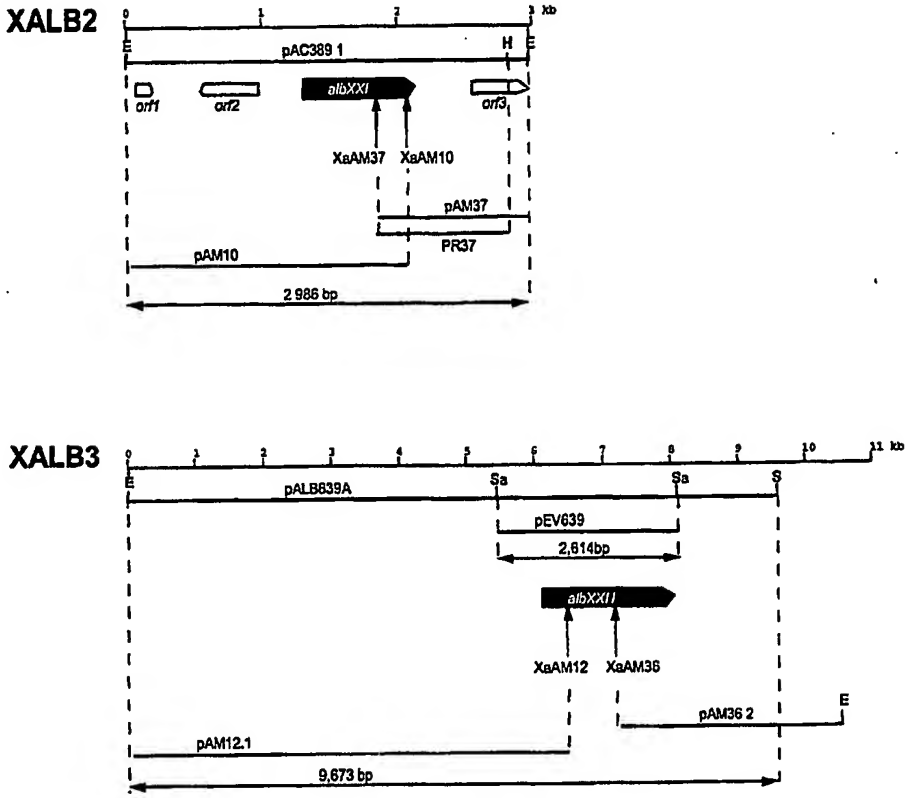


Figure 7B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0
1
2
3 kb
E
pAC389 1
H
E
orf1
orf2
albXXI
orf3
XaAM37
XaAM10
pAM37
PR37
pAM10
2 986 bp
XALB3
0
1
2
3
4
5
6
7
8
9
10
11 kb
E
pALB639A
Sa
Sa
S
pEV639
2,614bp
albXXII
XaAM12
XaAM36
E
pAM36 2
pAM12.1
9,673 bp

Figure 8

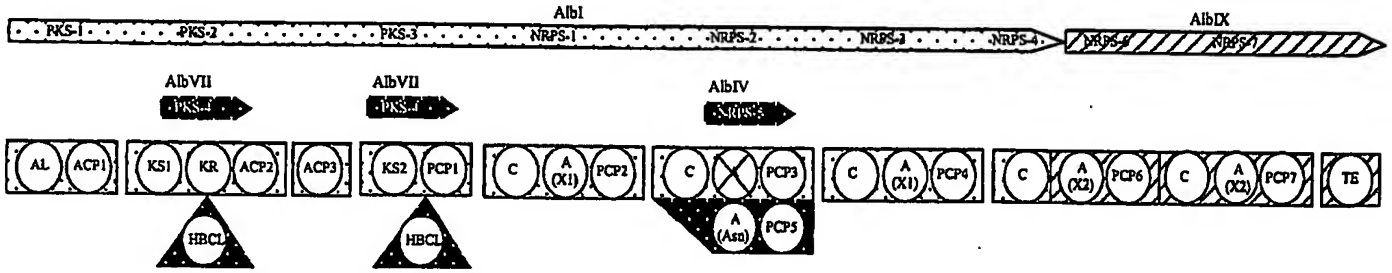


Figure 9A

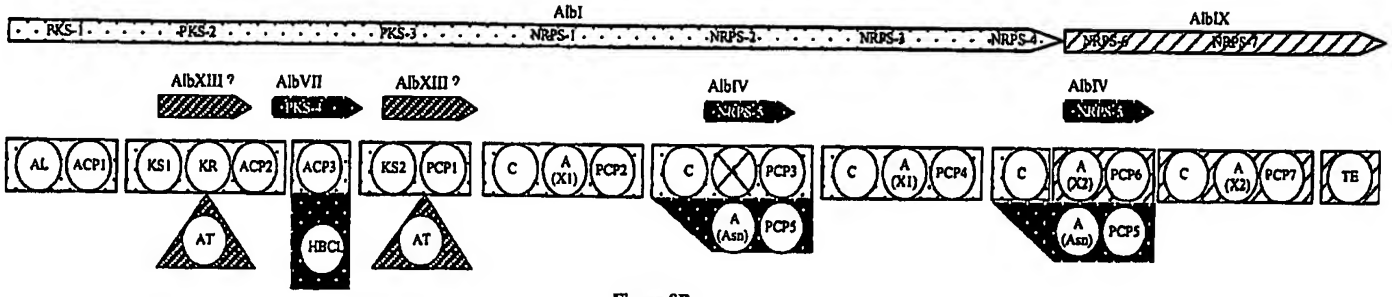


Figure 9B

```
RifA-1   LGRVDVLQPACFAVMVGLAAVWESVGVRPDAVVGHSQGEI
RifA-2   LDQTMYTQGALFAVETALFRLFESWGVRPGLLAGHSIGEL
RifA-3   LDRVDVVQPASFAMMVGLAAVWTSLGVTPDAVLGHSQGEI
RifB-1   LDRVDVVQPASFAVMVGLAAVWESVGVRPDAVVGHSQGEI
RifE-1   LNQTVFTGAGLFAVESALFRLAESWGVRPDVVLGHSIGEI
BlmVIII  ADDTRAAQPALFAVEYALARTLMDWGVRPAAMLGHSLGEV
```

Figure 10A

```
AlbXIII  LEDRPRHIRAVIDTLTGHAQFGPAIQAHNVAVIGHSVGGY
FenF     TRTMNAQPAILTVSVIAYQVYMQEIGIKPHFLAGHSLGEY
LipA     PDSRGRQLLAALDYLTGRSSVRGRIDSGRLGVMGHSMGGG
```

Figure 10B

Figure 11A: Putative substrates of PKS and NRPS modules

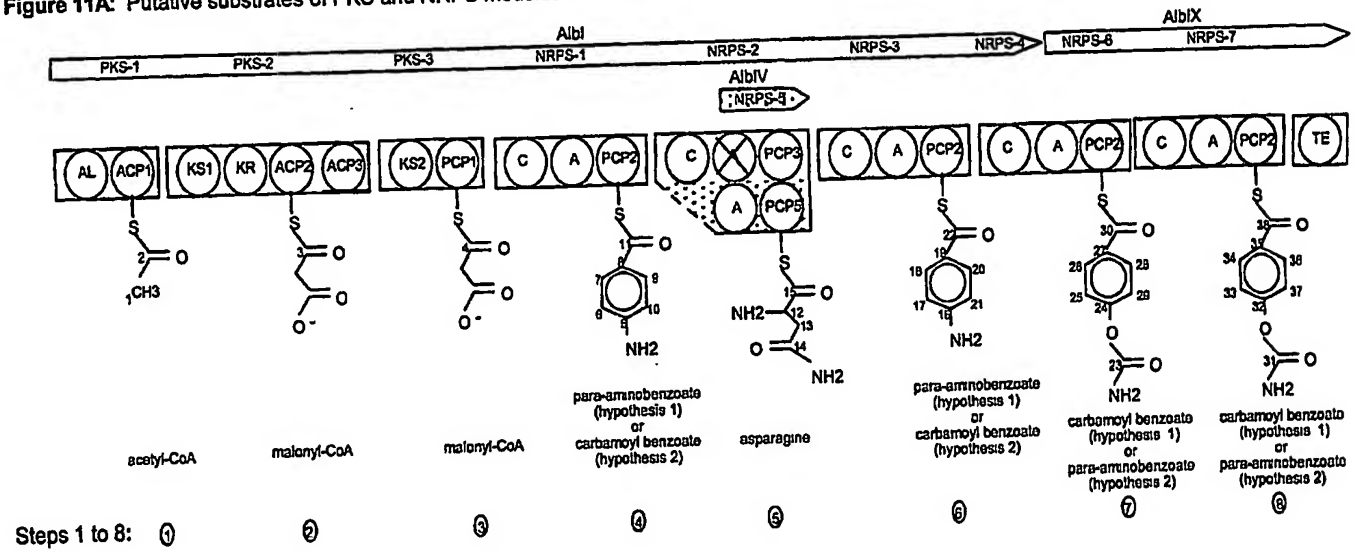
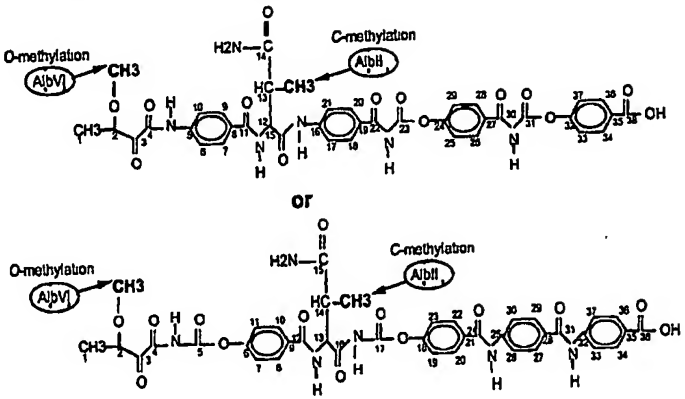


Figure 11B: Compositions and structures of albicidins



$C_{40}O_{15}N_6H_{35}$
(molecular weight : 839)